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ABSTRACT

This is one of several study guides on contemporary problems produced by the American Association for the Advancement of Science with support of the National Science Foundation. This guide focuses on the origin of man. Part I, The Biochemical Evidence for Human Evolution, contains four sections: (1) Introduction; (2) Macromolecular Data; (3) Discussion; and (4) Bibliography. Part II, The Fossil Evidence for Hominid Evolution, contains six sections: (1) The Evidence from South Africa; (2) The Evidence from East Africa; (3) Problems in Dating; (4) Problems in Interpretation: The Post-Cranial and Endocranial Evidence; (5) Problems in Interpretation: The Taxonomy of Early Hominidae; and (6) Bibliography of Miocene Hominoids. Each section includes a bibliography; most sections also include a variety of tables, figures, and graphs. (RH)

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TEST EDITION

(Unedited Copy)

ORIGIN OF MAN:
Problems in the Interpretation of New Evidence

by

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1975

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Since 1970 the American Association for the Advancement of Science has conducted the NSF Chautauqua-Type Short Courses for College Teachers Program with the support of the Education Directorate of the National Science Foundation. More than 9,000 college teachers of undergraduate students have participated in the courses which have dealt with either broad interdisciplinary problems of science or the applications of science and mathematics to college teaching. All of the courses are designed to make available the most current information.

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The test editions of the set of six Study Guides were prepared on relatively short notice by the course directors during the summer of 1975. To provide as much information as possible to the authors for use in revising this study guide for publication, we ask you as a participant in the NSF Chautauqua-Type Short Course to test these materials and provide your reactions. Also we would appreciate receiving reactions of your colleagues and students if that is possible. Your efforts will contribute significantly to the quality of the revised Study Guide.

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We hereby gratefully acknowledge the services of Joan G. Creager, Consulting Editor, and Orin McCarley, Production Manager for this series.

Arthur H. Livermore
Acting Director of Education
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AUTHOR'S PREFACE

The study of "man's" origins from a scientific point of view is a relatively recent discipline when one considers history or philosophy or even medicine, whose basis for study goes back to the earliest written records. Yet "man" has always wondered about "man" and attempts have been made throughout our history to account for our "place in Nature." The documentation of these attempts can be found in T. D. McCown and K. A. R. Kennedy's *Climbing Man's Family Tree*. It is this most important background information which, when understood, makes a good deal more sense out of the enormous amount of data we have to work with today in the attempt to address ourselves to the questions of our earliest origins.

It took so much work, so much effort against enormous prejudice to arrive at that right point in time where these problems could be considered scientifically. It began with Darwin and others of his time, Wallace, Huxley and Mendel, to name only a few, and it has not ended nor is any end in sight. Bernard Campbell has recently written that: "Paleoanthropology is becoming a real science at last, where analysis can precede hypothesis, and where progress takes the form of an orderly revision of the consensual working hypothesis. In this way, we move step by step up the ladder of induction to a better understanding of man's place in Nature" (Campbell 1973: 200).

Increasing numbers of scientists are turning their interests to the study of man's origins so that today paleoanthropology is the subject matter of biochemists, geologists, paleontologists, geochemists, botanists, zoologists and anthropologists. It is one of a few fields whose members come from the widest range of scientific disciplines.

This test edition is a reflection of the multidisciplinary approach to this study. It is an attempt to present as much of the published data as possible from a wide range of scientific endeavors. It could easily be larger for much of the important work of others has been trimmed and abstracted to the point, some may argue justifiably that some aspects of the state of the art are not fairly presented.

We have made the attempt, however, in this edition to represent most of the major contributions and have provided a bibliography for each section so that problems can be more clearly identified and investigated by the reader. We hope that the major contribution of this volume to the study of man is that it will be a valuable compendium of a wide variety of knowledge of other scholars presented by the authors, hopefully, without prejudice to a point of view. Its real value, however, is that it can be and will be periodically updated with the welcom assistance of all who read it.

The National Science Foundation and the American Association for the Advancement of Science are to be congratulated for providing the mechanism allowing this information to have wide distribution at minor cost. The authors wish to thank Ms. Lynn Condit and Ann Shofner for their time in preparing the manuscript and Ms. Gloria Pelatowski in the preparation of many of the edition's figures. We would also like to thank Shirley Strum whose contributions will appear in the final edition, to George Shkurkin whose subtle contributions appear throughout, to Professor Sherwood Washburn for his many inspirations before this project was ever envisioned, and to T. D. McCown in whose memory this effort is dedicated.

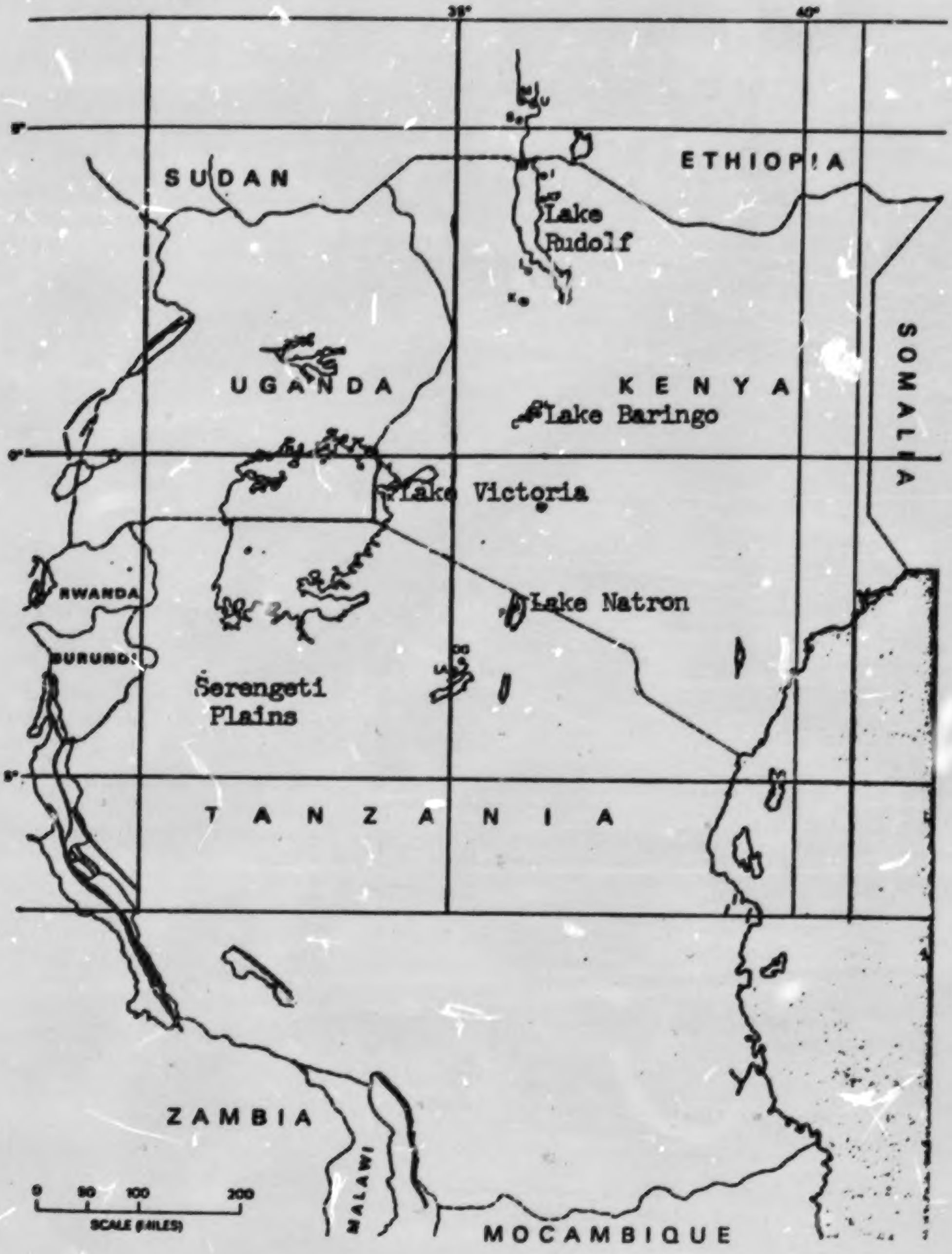
Figure II - i

Map of Plio/Pleistocene localities in Eastern Africa.

Figure II - ii

African Plio/Pleistocene geochronology. South African sites based on faunal correlations.

Figure II - i


35°
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SOMALIA
UGANDA
KENYA
Lake Baringo
Lake Victoria
RWANDA
BURUNDI
Lake Natron
OG
Serengeti Plains
TANZANIA
ZAMBIA
MALAWI
MOCAMBIQUE
0 50 100 200
SCALE (MILES)

Map of Pliocene/Pleistocene localities in Eastern Africa. North Lake Rudolf (lower Omo Basin): M (Mursi), U (Usno), S (Shungura) Formations. East Lake Rudolf: I (Ileret sector), KF (Koobi Fora sector). Southwest Lake Rudolf (Kerio Basin): L (Lothogam), K (Kanapoi). Lake Baringo (Baringo Basin): C (Chemeron), Ch (Chesowanja) localities. Lake Victoria (Kavirondo Gulf): K (Kanam). Lake Natron (Natron Basin): P (Peninj). Serengeti Plains: OG (Olduvai Gorge, La (Laetolil).

AFRICAN PLIO-PLEISTOCENE GEOCHRONOLOGY

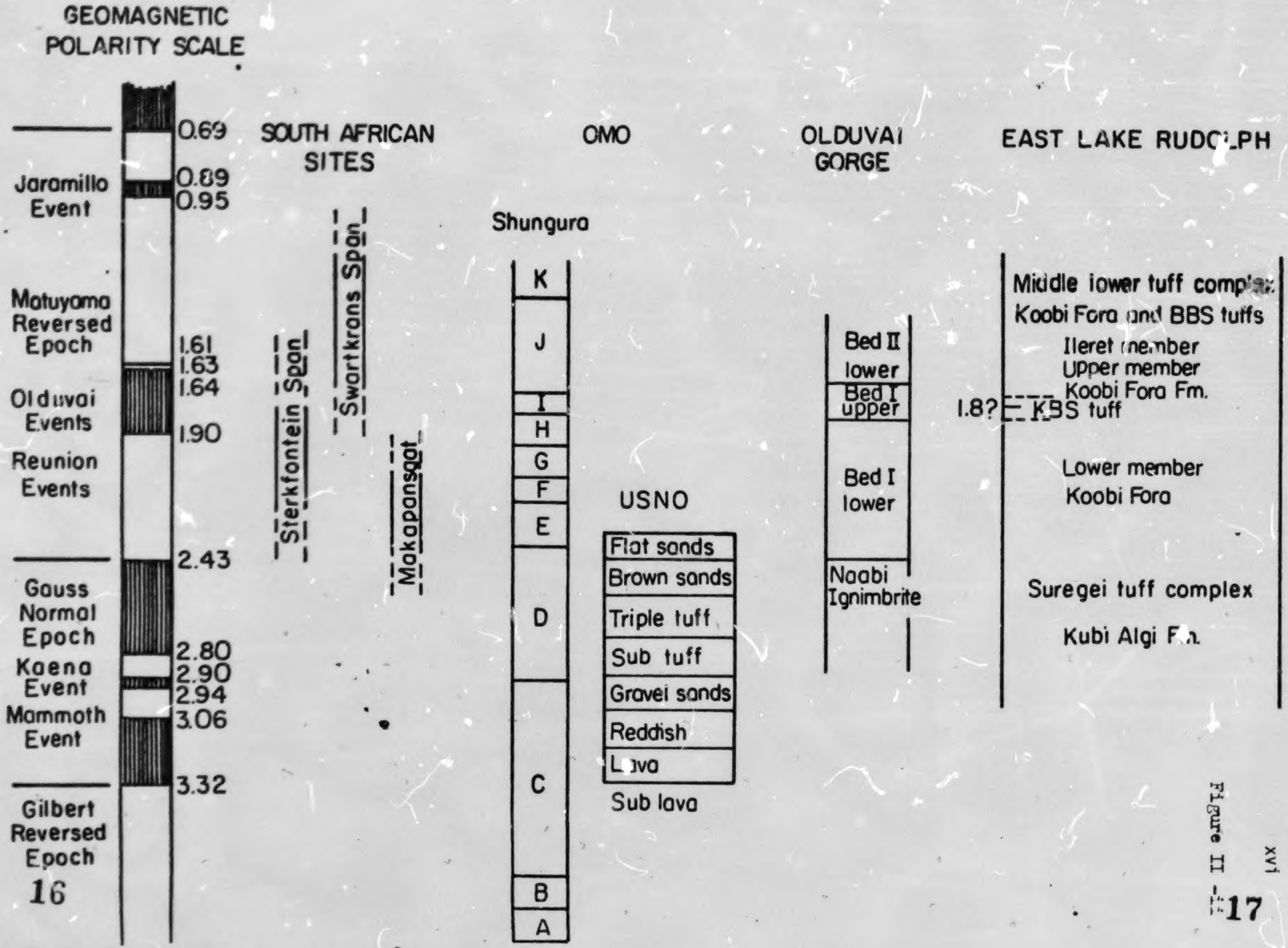

Figure II-17

A. INTRODUCTION

Why Study Macro-Molecules?

In order to fully understand how species differ from one another and how the various distinguishing characteristic features come to be, it is first necessary to place the species in a phylogenetic framework. Lacking this framework, it is impossible to expect to fully answer the how and the why questions concerning the evolution of a species. In the pursuit of the how and the why questions, evolutionary biologists draw from many sources of evidence. These include information from studies of the comparative anatomy of living species, from behavioral information, from evidence from the fossil record, and most recently from evidence drawn from comparisons at the macromolecular or biochemical level. In an ideal situation, all of these resources would be drawn upon before conclusions are reached on how an organism evolved. Each source of data has specific limitations and specific advantages, yet they may be used to complement one another in compiling a total evolutionary picture.

One of the most interesting as well as the most controversial of issues, today as well as historically, is the question regarding man's origin. What living form or forms is most closely related to man? What was the ancestral form like? Opinions merely regarding the temporal origin of man vary widely, ranging over a span of almost 30 million years. Kurtèn (1970) suggests man's lineage appeared approximately 30 million years ago in the early Oligocene, while Sarich and Wilson (Sarich and Wilson 1967b, Sarich 1968) have suggested that man's lineage separated from that leading to the african apes, chimpanzee and gorilla not much more than 5 million years ago. Other individuals take something of an intermediate stance (Simons 1972, Leakey 1969).

How you view Man's evolution depends on the following considerations; 1) what form is seen as being ancestral, 2) what the closest living relatives are, and 3) what the time of separation of these ancestral lineages are. There are a number of controversies which can be traced simply to what perspective an individual assumes. For example, there is a controversy over what morphological pattern is antecedent to the development of the bipedal locomotion that characterizes modern man. However, what locomotor pattern chracterized the ancestral proto-hominid? If man's lineage diverged from that leading to other hominoids in the earliest Oligocene then the ancestral locomotor pattern was probably arboreal quadrapedalism such as is seen in modern Old World monkeys. If hominids originated in the early to mid-Miocene, 15-20 million years ago, then the ancestral locomotor pattern may have been incipient brachiation. An origin of the hominid lineage in the late Miocene-early Pliocene, 4-8 million years ago, suggests that the ancestral form had for some period of time passed through a well developed brachiating stage (although probably not as well developed as it seen in the modern gibbon) and that the subsequent proto-australopithecines may have even passed through a knuckle-walking phase (Tuttle 1974, Washburn 1971).

The lack of an adequate fossil record and the debate engendered over various proposed ancestral hominids such as Ramapithecus (Simons

1972, Simons and Pilbeam 1965, Pilbeam 1966, Walker and Andrews 1973, Andrews 1974) or Kenyapithecus africanus (Leakey 1968b, Simons 1969) has forced students of man's evolution to rely primarily on comparative morphological and behavioral evidence. However, morphological similarities may be due to parallelisms or convergences rather than inheritance of traits from a common ancestor and similarities seen between living and fossil forms may be due to shared ancestral characteristics, similarities in grade, not due to the derivation of such shared traits along an inferred ancestral-descendent lineage (Delson 1974).

What is needed is a source of information that allows unambiguous answers or conclusions to be drawn regarding phylogenetic or temporal relationships. Comparisons between the proteins or nucleic acids of living species provide just such a source of data. The development of these techniques of comparison of macromolecules, some tracing back some seventy years (Nuttal 1902, 1904), has revolutionized the study of evolution. With the knowledge of how DNA is structured and the knowledge of the relationship of genes to polypetide chains, relatively unambiguous conclusions can be drawn as to phylogenetic relationships by assaying the nucleic acids or proteins of life forms.

Molecule evidence is now rapidly accumulating concerning the actual phylogenetic position of man vis a vis the other primates. The data suggests that man is closely related to the chimpanzee and gorilla, the great apes, and that the latter are not more closely related to each other than either is to man (Goodman 1961, Hafleigh and Williams 1966, Sarich and Wilson 1967b, Kohne 1970, King and Wilson 1975, Sarich 1968, 1971, Cronin 1975, Cronin and Sarich in preparation). Man and chimpanzee are so close that they differ by only about 1-2% in their DNA sequence (Kohne 1970, Hoyer *et al*. 1972). This is an extremely close relationship, similar to the DNA differences seen between groups of baboons of the genera *Papio* and *Theropithecus*. The morphology of human and chimpanzee is quite distinct. Yet, it is also quite apparent that there are many similarities, especially in the thorax and upper limb areas. This was recognized over 100 years ago. T. H. Huxley concluded, in 1863, that "every bone of a Gorilla bears marks by which it might be distinguished from the corresponding bone of a man; and that in the present creation, at any rate, no intermediate link bridges over the gap between *Homo* and *Troglodytes*. It would be not less wrong than absurd to deny the existence of this chain; but it is at least equally wrong and absurd to exaggerate its magnitude, and, resting on the admitted fact of its existence, to refuse to inquire whether it is wide or narrow." We now know that this chasm is both narrow, at the genetic level, and relatively wide at the morphological level.

In addition, regarding temporal considerations, the molecular data can be interpreted to suggest that humans and chimpanzees may have diverged approximately 5 million years ago (Sarich and Wilson 1967b, King and Wilson 1975, Sarich and Cronin 1975 in press). This conclusion suggests that the ancestral morphotype of the common ancestor of the African apes and man may have resembled a modern day chimpanzee (Sarich 1968), or even more closely a pygmy chimpanzee (Pan paniscus). And, the method of locomotion employed by this common ancestor was a knuckle-walking form of terrestrial locomotion derived from an ancestor capable of full brachiation, as Washburn has previously suggested based purely on morphological criteria (Washburn 1968). Natural selection would have presumably acted with rapidity in order to adapt the protohominids for efficient bipedalism. By approximately 3 M.Y. ago Australopithecus was essentially fully bipedal (Zihlman 1970). Additionally, the molecular data lead to implications for interpreting the fossil record. If a hominid lineage did not exist until 5 million years ago then, clearly, Ramapithecus cannot be a hominid. Thus, the use of comparative molecular data allows inferences to be drawn concerning morphological or fossil evidence, and in the case of man's evolution allows a clear cut choice among extreme alternatives.

What is it about comparative protein and nucleic acid studies that makes them potentially so useful in solving evolutionary relationships? The answer is that these macromolecules possess two uniquely useful properties not characteristic of any other source of comparative information. The first is their ubiquity--all primates have albumins, transferrins, hemoglobins, and DNA's of very similar, if not identical, function and basic structure. Secondly, the unit of evolutionary change involved in producing the differences seen among these molecules in different taxa--amino acid or nucleotide substitution-is known. Thus, it is possible to compare functionally equivalent and evolutionarily homologous entities among very diverse taxa simply by counting these substitutions. The problem, of course, lies in developing appropriate methods of counting and relevant modes of interpreting the data so obtained.

The four basic methods, to be discussed below, are amino acid or nucleotide sequencing, nucleic acid hybridization, electrophoresis, and lastly, immunology, each with its own utility in providing quantitative macromolecular comparisons. The data such comparisons provide vary in the ease of obtaining them, in the taxonomic levels at which they are useful, and in the fidelity with which they accurately reflect the actual substitutions which occurred along the lineages leading to the modern species being studied.

Using these techniques, the differences in eith proteins or nucleic acids can be measured and a distance matrix can be generated. Once this is done, there are methods by which the matrix can be converted into a phylogeny. A phylogeny has three basic components. The first is cladistics. This is the branching or diverging order of the lineages. The second component is called patristics. This is the evolutionary change occurring along a lineage such as the development of bipedalism or even the number of amino acids substituted in a particular protein along a branch of a cladogram. The third component is chronistics. This is the time of separation of the various lineages. Calculating these times of divergences from the molecular data depends on the observation that molecules evolve at a statistically constant rate. This was first noticed by Zukerdandl and Pauling (1962, 1965) and further developed by Sarich and Wilson (1967a, 1967b, 1973) among others. If a certain reference point (a calibration point) is chosen from the fossil record for two species whose genetic distance is known, then if the molecule evolved at a constant (non-deterministic) rate, the molecule can serve as an evolutionary clock. Thus, approximate times of divergence of species can be calculated where only a genetic distance is known.

Proteins have within them a history. Their amino acid sequence must have followed an evolutionary pathway that can be deduced. Therefore, it should be possible to construct cladograms by counting the differences among the homologous molecules of various species. Secondly, if the amount of change can be correlated with absolute time, a time scale can be added to the cladistic framework. Thus, each animal has within it its own evolutionary genealogy and with the proper skills it is possible to translate this encoded genetic information into a quantitative phylogeny.

Macromolecules in Systematics

Beginning with the pioneering work of Nuttall (1902, 1904) macromolecules have become an increasingly powerful source of data in probing evolutionary relationships. As knowledge of mechanisms of evolution grew and with the advent of better techniques macromolecules became more and more useful. There are now four basic major techniques employed in ascertaining genetic relationships as revealed by macromolecular differences. All are useful, but are appropriate at different times to different questions or problems. The methods are: 1) amino acid sequencing; 2) DNA hybridization; 3) electrophoresis; and 4) immunology.

Amino acid sequencing has now been used to determine the primary structure of many proteins. A few that have been useful in molecular systematics of mammals are: cytochrome C (Fitch and Margoliash, 1967; Dickerson, 1971, 1972), fibrinopeptides (Doolittle _et_ _al_., 1971; Wooding _et_ _al_., 1972), lysozyme (Prager and Wilson, 1971a, b), haemoglobin (Zuckerkandl, 1965; A[illegible] _et_ _al_., 1971; Goodman _et_ _al_., 1973, 1974; Matsuda _et_ _al_., 1973 a, b, c), and myoglobin (Air _et_ _al_., 1971, Romero-Herrera _et_ _al_., 1973). Once the sequences of a number of homologous proteins are known, one can construct a cladogram of the various lineages. Fitch and Margoliash (1967) have analyzed the sequences of over twenty cytochromes C from eukaryotic organisms and have developed a phylogeny for these organisms. Recently, both Fitch (1973a, b) and Dayhoff 1969a, b; 1972, 1973) have extended this cladogram as more sequences became available from various other taxa. Goodman _et_ _al_. (1971, 1973, 1974) have generated extensive mammalian phylogenetic trees using haemoglobin sequences.

The technique is extremely useful, potentially surpassed only by base sequencing of the DNA itself for constructing phylogenetic trees, as proteins only partially reflect DNA base sequence due to the degeneracy of the genetic code. There are a few drawbacks with this technique. It is extremely time consuming. A large molecule of 500 amino acids may take years to finish. It can be uneconomical of material, and from certain species such as Daubentonia, it may be impossible to collect enough material to do a proper sequence. It is also impractical to consider using it to do an intensive systematic survey of a selected group, given the present state of the technique.

The second and most recent method of determing genetic affinity of organisms is nucleic acid hybridization. This technique has been employed by Kohne (1970), Hoyer et al. (1972), Laird, McConaughy and McCarthy (1969) and Kohne et al. (1972). DNA, when sheared or fragmented and heated to an appropriate temperature, will separate into its two constituent chains. Upon subsequent cooling, the chains will reanneal or reassociate into their proper configuration with pairing occurring between opposite complementary strands. The degree to which heterologous DNA reanneals compared to the native or homologous DNA is a measure of the relatedness of the two sequences of DNA being compared. The differences may be measured as a ΔTm (change in thermal stability) and expressed in terms of a per-cent base pair mismatch. The greater the base pair mismatch the lower the melting point of the hybrid DNA molecule. Kohne et al. (1972) and Hoyer et al. (1972), have employed this method to construct cladograms of this single character measurement for the primates with particular reference given to hominoids.

Intrinsically, this method is extremely useful as one is supposedly viewing the entire genome of an organism. However, there is both a close and a distant limit to what one may measure. The method is insensitive for interpopulation (deme) distances or even closely related species although it gives the indication one is looking at closely related organisms. The distant limit is within a mammalian order. For instance, the Homo-Galago relationship which is a comparison between suborders, is at or beyond the limit of the method. Obviously one could not attempt to do cross ordinal, class or even phylum comparisons as have been done with various slowly evolving proteins. Extensive surveys of taxa are expensive in both time and material.

The third technique, electrophoresis, is currently the most popular method employed by evolutionary biologists. Proteins are placed in an electric field in a particular suspensory medium (starch or acrylamide). Proteins coded by a specific locus, may have different net charges and will be discriminated by differential migration in this medium. Since the original population genetics oriented work of Lewontin and Hubby (1966a, b), the technique has proved useful in the study of genetic variability of populations including gene frequency analysis and individual heterozygosity. The method in recent years has proved extremely popular and it has been extended from measuring differences between populations to higher taxonomic categories. Various animals and plants have been surveyed electrophoretically including Drosophila (Ayala et al., 1972 a, b), Avena (Allard et al., 1972; Clegg et al., 1972a, b; Hamrick and Allard, 1972), rodents (Selander et al., 1969, 1973; Johnson and Selander, 1971), non-human primates (Weiss, 1972; King, 1974; King and Wilson, 1975) and humans (Harris, 1966; Nei, 1971, 1972).

The method has its maximum utility at lower taxonomic levels. Eventually, all the proteins will have accumulated charge changes and a maximum differentiation will have been attained. Thus there is a genetic distance limitation to the method. One should survey many loci and should attempt to screen as many individuals as possible from the group or groups in question so that one maximizes the likelihood of viewing all the polymorphisms present. Once the raw data are generated, methods of converting them into distance measurements are available (Selander, 1969; Nei, 1971, 1972). Nei's ideas are intriguing, for given certain assumptions concerning the rate of substitution of certain molecules and the proportions of mutations which lead to charge changes, one is able to convert distance measurements into a time scale. In any case, a relative scale is deduced from the raw data alone without the addition of a time dimension.

Beyond the genetic distance limitation, a large amount of variability is missed, for with a random distribution of mutations, only about one in four yields a charge change. Also, charge may be conserved evolutionarily as Sarich (1972) has demonstrated in detecting immunological differences among carnivore haemoglobins from different taxa that were electrophoretically identical. Overall net charge may remain constant as the primary sequence varies. As a technique, electrophoresis underestimates the amount of variability within a population.

The fourth general method useful in studying evolutionary relationships is immunology. Basically, antibodies are produced in a host animal to an antigen and then similar (homologous[1]) molecules are reacted with the antibodies and the amount of reaction is measured. The standard one needs to refer to is the amount of reaction of the antibodies and the molecule that they are directed against. Antibodies recognize best the antigen to which they are directed against, and recognize less well a homologous antigen that has changed somewhat--e.g., the same protein in a related species. The greater the sequence difference, the less the recognition. Until recognition is completely lost when there is 35-40% sequence difference. Thus one has a general scale of difference and this has been recognized since the early twentieth century in Nuttall's work (1902, 1904). Williams (1964) has an excellent discussion of the uses of the immunological approach to protein evolution.

A standard technique has been quantitative precipitation, where the amount of precipitation is measured when antibodies are complexed with antigen in large amounts. It is possible to measure relative differences from the homologous[2] antigen antibody reaction when a specific antibody is reacted with a heterologous antigen. Nuttall observed that the degree to which the reaction lessened was correlated with taxonomic distance, Hafleigh and Williams (1966) made similar observations. Sarich (1972b) has employed this technique in his extensive surveys of marsupials, rodents and carnivores. Weigle (1961) has reported on ungulate albumins and Wang _et al_. (1968), using inhibition techniques, have studied primate transferrins.

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[1] Homologous in this sense means molecules that share ultimately a common ancestral gene.

[2] Homologous in this sense may be defined as the antigen that the antisera is directed against. Heterologous is any antigen other than the one the antisera is directed against, although these heterologous antigens are homologues of the antigen to which the antisera is directed.

A second technique involves the observation of precipitation lines between antibody and antigen in an agar gel (Stollar, 1963). The antibody and antigen are each placed in a separate well cut in the gel. Diffusion occurs and upon antibody recognition of an antigen, a precipitation line will form. Mohagheghpour and Leone (1969) and Bauer (1970, 1973) have employed this method in studies of primate proteins. Goodman (1961, 1962, 1963a, b) and Goodman _et al_. (1971) has also employed this method in his extensive studies of primate relationships.

The last immunological technique to be described is microcomplement fixation which was developed by Wasserman and Levine (1961). It involves the measuring the amount of complement (a series of enzymes found in vertebrate serum; Mayer, 1973) fixed or trapped in the antigen and antibody matrix while suspended in a buffer solution. Using antisera produced to a specific protein, the difference between the homologous and heterologous antigens can be measured with this technique. The difference between the homologous and heterologous antigens can be measured with this technique. The difference between the two antigens can be expressed as the degree to which the antibody concentration must be increased with the heterologous antigen as compared to the homologous antigen in order to fix equal amounts of complement in the antigen antibody matrix. This measurement has been called the Index of Dissimilarity (I.D.) (Wilson et al., 1964). The I.D. increases as genetic distance increases, and Prager and Wilson (1971a, b) have shown a direct correlation between I.D. and the number of amino acids substituted in avian egg white lysozymes. Similar results have been obtained with azurin and ferredoxin (Champion et al., 1973). Various proteins have been used as antigens and now quite a few taxonomic groups have been investigated. These include: 1) serum albumin, perhaps the most widely employed molecule, in primates (Sarich, 1967, 1968, 1970, 1971, 1972b; Sarich and Wilson, 1966, 1967a, b; Wilson and Sarich, 1969; Cronin and Sarich, 1975), carnivores (Sarich, 1969a, b, 1972a, 1973, 1974), rodens (Sarich, 1972a; Keeler and Sarich, unpub. obs.), anurans (Wallace, 1971; Wallace et al., 1971, 1972, 1973; Maxson, 1973; Maxson and Wilson, 1974, 1975), reptiles (Gorman et al., 1971; Wyles and Sarich, unpub. obs.); 2) lysozymes in birds (Prager and Wilson, 1971a, b), primates (Hanke et al., 1973); 3) carbonic anhydrase in primates (Nonno et al., 1969); 4) lactate dehydrogenase in vertebrates (Wilson and Kaplan, 1964; Gorman et al., 1971; 5) azurin in bacteria (Champion et al., 1975); 6) ferredoxin in bacteria (Champion, 1972); 7) alkaline phosphatase in bacteria (Cocks, 1971; Cocks and Wilson, 1969, 1972; for other microcomplement fixation studies of bacterial protein evolution see Steffen _et al_., 1972; London and Kline, 1973; for references) and lastly, transferrins in primates (Cronin and Sarich, 1972, 1973a, b, 1974), rodents (Sarich, unpub, obs.), carnivores (Sarich, 1973 and Sarich, unpub. obs.), and birds (Prager _et al_., 1974).

The method described above, microcomplement fixation, has many advantages. It is sensitive, often being able to detect single amino acid substitutions (Cocks and Wilson, 1969; Cronin, 1975). It is economical, using only microgram quantities of material. Extensive surveys of many groups can be carried out in a relatively short period. The antigen need not be purified as whole serum can be used as the heterologous antigen source (Sarich, 1967). Also, the technique is capable of being employed over wide taxonomic distances such as within and between orders of mammals, among orders of birds, and within superfamilies of frogs and reptiles.

Microcomplement fixation has a few limitations. The position of substitutions in the molecule cannot be known as internal substitutions are not visible to the antibodies and thus cannot be measured. However, a great majority of substitutions are external and thus visible (Dickerson, 1971, 1972). Moreover, the sequence-immunology correlation is only approximate. Antibodies also fail to recognize as homologous those molecules which have evolved or changed approximately 40% or more of their sequence (Prager and Wilson, 1971a, b). Those molecules which evolve rapidly have a limited utility for determining genetic distances at higher taxonomic levels. In addition, there are problems of unknown dimensions. The first of these is the problem of changes in the structure of the molecule other than amino acid substitutions including deletions and partial duplications, etc., or differences in prosthetic groups such as carbohydrate side chains could arise. Secondly, conformational changes could occur during the course of the functioning of the molecule which might cover or expose antigenic determinants. Differences could also be due to post-translational modification as has been reported for mouse serum albumin (Wilcox, 1973). The possibility exists that differences other than in the primary sequence could produce immunologically detectable differences. Certain of these problems are discussed for the anti-gransferrin-transferrin system under the section entitled transferrin structure. The method, on the whole, is good for systematic work without being as time consuming as sequencing, or as complex as DNA hybridization: and is able to survey taxa at higher levels that are beyond the range of electrophoresis.

Evolutionary Clocks

The idea that molecules might serve as evolutionary clocks was proposed by Zuckerkandl and Pauling in 1962, (see also Zuckerkandl, 1965) based upon their investigation of haemoglobin structure. This hypothesis was further strengthened by work done by Margoliash (1963), Smith and Margoliash (1965), Salthe and Kaplan (1966) and Sarich and Wilson (1967a, 1967b, 1973; Wilson and Sarich, 1969). Sarich and

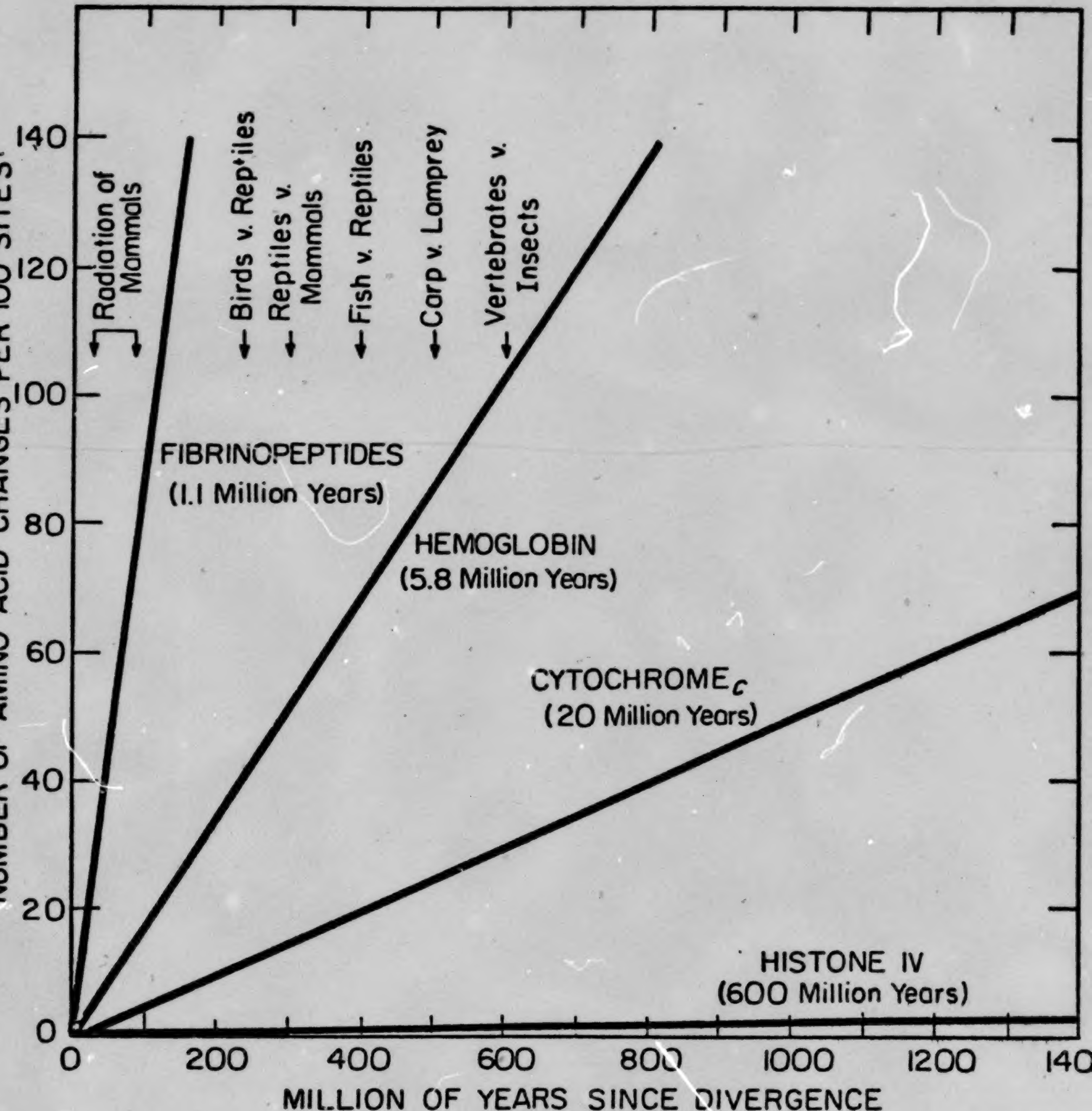
Wilson observed that along different branches of a phylogeny there seemed to be about equal amounts of change, as measured by micro-complement fixation technique. This observation of regularity of protein evolution could be explained by describing evolutionary substitution occurring in a protein molecule as being stoichastic. That is, when the number and distribution of these evolutionary events were known, they would fit a Poisson distribution. Certain portions of the molecule could accept more changes and would tend to vary together (covarions) (Fitch and Margoliash, 1967; King and Jukes, 1969).

Different molecules have different rates of evolution, and a standard has been defined as the Unit Evolutionary Period (U.E.P.). This is the time necessary for a one per cent (1%) change in sequence difference to develop between homologous macromolecules of two diverging lineages. The unit evolutionary period is 20 M.Y. (million years) for cytochrome C, 1.1 M.Y. for fibrinopeptides, 6 M.Y. for histone (IV), (Dickerson, 1971, 1972; Dayhoff, 1972) Figure I - 1. For serum proteins the unit evolutionary period is fairly short. Albumin, based on sequence work (Brown, unpub. obs.) and immunological data (Sarich, 1967a, b; Sarich and Wilson, 1967a, b; Wallace et al., 1971; Maxson and Wilson, 1974) has a unit evolutionary period of about 2.5-3.0 M.Y. Serum transferrin has a unit evolutionary period of approximately 2 M.Y. (Mao and Dessauer, 1971; Cronin and Sarich, 1972, 1973).

Figure I - 1

Rates of evolution of proteins can be calculated by plotting average distance in amino acid sequences between species on two lineages whose divergence event can be dated. Divergence dates are drawn from the fossil record. Adapted from Dickerson (1972).

FIGURE 1-1


NUMBER OF AMINO ACID CHANGES PER 100 SITES
0
20
40
60
80
100
120
140
0
200
400
600
800
1000
1200
140
MILLION OF YEARS SINCE DIVERGENCE
Radiation of Mammals
Birds v. Reptiles
Reptiles v. Mammals
Fish v. Reptiles
Carp v. Lamprey
Vertebrates v. Insects
FIBRINOPEPTIDES
(1.1 Million Years)
HEMOGLOBIN
(5.8 Million Years)
CYTOCHROME$_c$
(20 Million Years)
HISTONE IV
(600 Million Years)

Molecules have become widely used as molecular clocks in recent years and have been used to date the divergence times of invertebrates and vertebrates (Goodman *et al*., 1974), amphibians (Salthe and Kaplan, 1966; Wallace *et al*., 1971, 1973; Maxson and Wilson; 1974, 1975), reptiles (Gorman *et al*., 1971; Mao and Dessauer, 1971), carnivores (Sarich, 1969a, b), primates (Sarich, 1966, 1968, 1970; Sarich and Wilson, 1967a, b; Wilson and Sarich, 1969; Goodman *et al*., 1970), marsupials (Sarich, unpub. obs.; Air *et al*., 1971) and micro-organisms (Cocks, 1971; Champion, 1972).

This observation of the seeming regularity (in a probabilistic sense) of protein evolution has caused extensive controversy, yet a plausible explanation has been offered. King and Jukes (1969), Kimura (1968, 1969), Kimura and Ohta (1971a, b), Ohta (1972) and Ohta and Kimura (1971a, b, c) have hypothesized that some portion of the mutations occurring at the DNA level are neutral at the level of the protein (in terms of allele fitness) and that these new alleles can be incorporated into the population, and even fixed by genetic drift. Neutral substitutions are substitutions in the polypeptide chain in a position where more than one specific amino acid may be inserted without conferring either a selective advantage or disadvantage on the new allele. These calculations were originally based upon the supposed rate of mutation and the projected substitutional load. Various authors have criticized the concept of netural mutation and have inferred that selection would indeed be operating upon every allele substitution (Smith, 1968; Clarke, 1970a, b; Arnheim and Taylor, 1969; Richmond, 1970). Uzzell and Corbin (1971, 1972) have published an alternative distribution curve, postulating that a negative binomial instead of a Poisson has a better fit to the observed distribution of changes at the codon level. Specific criticisms suggest that not all lineages show the same amount of evolution among them. Jukes and Holmquist (1972) noted a non-constancy of evolutionary rates of rattlesnake cytochrome C. Penny (1974) while taking specific issue with Jukes and Holmquist's observations, finds that rates along lineages vary greatly and thus pose a serious problem to the hypothesis of regularity of protein evolution. Langley and Fitch (1974) also see quite a large variation in rates of nucleotide substitution throughout vertebrate evolution.

In the specific case of primate evolution, various authors question the regularity of rates of evolution for various molecules. Goodman (Goodman, 1961, 1962, 1973a, b; Goodman _et al_., 1971, 1973, 1974) is primarily responsible for postulating a placentation effect seen in the deceleration in the rate of protein evolution for those organisms with increased maternal fetal contact. Hoyer (Hoyer _et al_., 1972), Kohne (Kohne _et al_., 1972 and Lovejoy (Lovejoy _et al_., 1973) have all postulated a generation time effect with similar deceleration in the rate of protein evolution for those organisms with long generation times, in order to reconcile paleontological estimates of times of separation of taxa and the biochemical differences. This latter generation effect argument has been countered by Sarich (1972b) and Sarich and Wilson (1973).

B. MACROMOLECULAR DATA

The following section will present the molecular evidence concerning the phylogenetic relationships within the primates with emphasis on man and his closest relatives, the apes, the taxonomic unit Hominoidea. There will be a brief explanation of each method coupled with the presentation of the raw "genetic distances" and a method of conversion of the data into a phylogenetic tree construction can be found in the references. The data will be organized by techniques and presented in the sequence electrophoresis, DNA hybridization, immunology, and lastly protein sequence.

1. Electrophoresis

Electrophoretic data that provides phylogenetic information within primates is relatively limited. There are quite a few studies that detail specific polymorphisms in specific groups of primates but these contain little comparative information for evolutionary purposes (Anderson and Giblett, 1975; Barnicot and Cohen 1970; Barnicot and Hewett-Emmett 1971, 1972; Barnicot and Wade 1970). For a summary of human serum protein or red cell proteins polymorphisms see Giblett (1969).

One key paper that does provide us with genetic distance and thereby phylogenetic information is the study by King and Wilson (1975). This paper details the average amino acid sequence difference between chimpanzee and man using electrophoretic criteria. The authors surveyed the electrophoretic mobility of 44 different structural genes of almost 100 chimpanzees. They subsequently compared the frequencies of the alleles at each locus with published reports of human allelic frequencies at the same loci. Of the 44 loci, 31 code for intracellular proteins and 13 code for secreted or extracellular proteins.

The symbol S represents the probability that human and chimpanzee will be electrophoretically identical at a particular locus i is

$$S_i = \sum_{j=1}^{A} X_{ij} Y_{ij}$$

where X_{ij} is the frequency of the jth allele at the ith locus in human populations and Y_{ij} is the frequency of the jth allele at the ith locus in chimpanzees.

The results are that about half of the proteins in the survey are electrophoretically identical for the two species and about half of them are different (Table 2, King and Wilson 1975). A few loci are highly polymorphic in both species. The proportion of alleles at an average locus that are electrophoretically identical in human and chimpanzees populations is about 0.52. Furthermore, if it can be assumed that at a particular protein, amino acid substitutions have occurred independently and at random with respect to species since human and chimpanzee diverged then the number of proteins that have accumulated amino acid substitutions since the divergence approximates a poisson distribution. Calculations from the data reveal that the average human protein is more than 99% identical in amino acid sequence to its chimpanzee homolog.

The actual human and chimpanzee genetic distance is about 0.62 using an index developed by Nei and Roychoudbury (1974). That is, there is an average of 0.62 electrophoretically detectable codon differences per locus between human and chimpanzee proteins. This degree of genetic distance is incredibly small given the major morphological and behavioral differences seen between humans and chimpanzees. This value corresponds to genetic distances found between Sibling species of Drosophila or mammals. Nonsibling species, or congeneric species, differ more from each other by electrophoretic criteria, than humans and chimpanzees. The human-chimpanzee distance exceeds populational differences found within species.

2. DNA Hybridization

There are relatively few studies using the techniques of nucleic acid hybridization that have relevance for understanding human or non-human primate evolution. The following data is drawn from Kohne (1970), Kohne et al. (1972), and Hoyer et al. (1972).

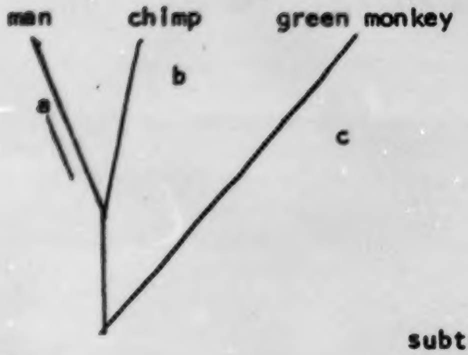
The procedure begins with the purification of DNA from an organism. The purified native DNA, which exists as a long linear polymer of nucleotide bases arranged in a double helix of paired complementing strands, can be readily separated into two single strands by the use of heat. Given the proper conditions, the DNA will reassociate and reform a stable double strand DNA molecule almost, if not exactly, identical to the original native DNA. This ability to reform into the original structure is a consequence of the property of sequence recognition. This is a property that is extremely useful in comparing the genetic material of different organisms.

The actual mechanical procedure usually employs the use of a column of hydroxyapatite crystals. Under certain conditions hydroxyapatite will absorb double strand native or hybrid reassociated DNA. Single strand DNA (unhybridized into a duplex) will not be absorbed and will pass through the column. The double stranded DNA can be removed from the column by the use of heat which breaks the hydrogen bonds that hold the strands opposite each other. The thermal stability of the native double strand DNA can be measured and can be used as a standard to measure the degree of perfection of base pair mtaching between strands of DNA from different organisms. The native DNA will disassociate into single strands at a specific repeatable temperature. The greater the difference between two organisms DNA the more imperfect the base pair matching in the hybrid duplex. Thus, there are less hydrogen bonds holding the complementary strands together. The less hydrogen bonding, the less energy in the form of heat is needed to disassociate the two strands (Table I - I).

For example, the thermal stability of the native reassociated human-human duplex DNA is 82.6°C. The hybrid man-chimp duplex disassociates at 81.2°C, a difference of 1.4°C in thermal stability. Since man and chimpanzee last shared a common ancestor the DNA sequences have diverged. The greater the phylogenetic distance between two species the greater the mismatch in base pairing. The human-green monkey hybrid is 6.3°C less stable while the human-capurbin hybrid is 10°C less stable than the native human duplex (capucin is a new world monkey).

From a number of experiments using DNA's of known compositional differences, a standard has been calculated such that a 1°C lowering of temperature in measuring thermal stability is caused by approximately a 1.5% difference in base pair sequence between two organisms DNA's. Thus, chimp and human DNA differ by about 2.4%. Human and green monkey differ by about 9.5%. Human and capucin differ by about 15.8% in their DNA sequence. Tables 1-2 and 1-3 present the data from Kohne et al. (1972) and Hoyer et al. (1972) respectively.

The raw data can be converted into a cladogram. Using a series of simultaneous equations the branch lengths or the amount of DNA sequence change expressed as a percentage can be calculated. For example, man and chimp differ by 2.4%, man and green monkey by 9.6%, and chimp and green monkey by 9.6%. Let man, chimp and green monkey be a, b, and c respectively.



We know a+b = 2.4%, a+c = 9.6% and b+c = 9.6% by direct observation.

Thus -

1)
$a+b = 2.4$
$\underline{b+c = 9.6}$
subtract $a-c = -7.2$

2)
$a+c = 9.6$
$\underline{a-c = -7.2}$
add $2a = 2.4$
$a = 1.2$
$\therefore b = 1.2$

Since man and chimp separated each has undergone about 1.2% base pair substitution. With this procedure most of the lineage lengths can be solved. Figure 1-6 presents the cladograms obtained from the data from Tables 1-2.

3. Immunological techniques

Immunodiffusion experiments.

Goodman has employed this technique in extensive studies of primate relationships (Goodman 1961, 1962, 1963 a, b; Goodman et al. 1971; Baba and Goodman 1975; Dene et al. in press). Others have also used this method (Bauer 1970, 1973; Mohagheghpour and Leone, 1969). A detailed account of the procedure may be found in Goodman and Moore (1971).

Briefly, the amount of similarity between two different macromolecules may be approximated using antisera to one of them. The procedure entails observation in agar gel of the intensity of precipitation of antigen and antibody and the extent of non shared antigenic distance reflected in spur size,

TABLE I-2

Extent of Nucleotide sequence change (Kohne _et al_., 1972)

DNA's reacted	Thermal Stability (T.S.) (°C)	.T.S. (°C)	Percent nucleotide substitution since divergence
Man-Man	82.6	0	0
man-chimp	81.2	1.5	2.4
man-gibbon	79.1	3.5	5.3
man-green monkey	77.5	6.3	9.5
man-capucin	72.1	10.5	15.8
man-galago	55.0	28.0	42
man-rat	-		
Green monkey (G.M.)-G.M.	84.4	0	0
G.M. - rhesus	82.4	2.0	3.0
G.M. - man	78.0	6.4	9.6
G.M. - chimp	78.4	6.4	9.6
G.M. - gibbon	78.3	6.4	9.6
G.M. - capucin	73.4	11.0	16.5
G.M. - galago	56	28.0	42.0
Mouse - mouse	85.7	0	0
mouse-rat	67.7	18.0	27.0
cow-sheep	77.0	6.0	9.0
cow-pig	69.0	14.0	21.0

TABLE 1-3

Relate thermal stabilities of human and organ DNA sequence reassociated in the presence of primate DNA fragments.

Hybrid DNA*

Reference Species	Human	Chimpanzee	Gorilla	Orang	Gibbon	Green monkey
Human	0	0.7	1.4	2.9	2.7	5.7
Orang	1.9	1.8	2.3	0	2.4	4.3

*hybrid molecule is composed of 1 strand of the reference species and a strand of a heterologous species. The relative thermal stabilities of the hybrid molecule are expressed as degrees centigrade difference from the native DNA thermal stability.

Goodman has developed a scale to quantify the degree of difference. Using multiple comparisons and set theory logic (Moore and Goodman 1968) a computer program translates spur size and intensity into a table of antigenic distances between two species. The results obtained from many comparisons are briefly summarized in Table 1-4. Results from Wang _et al_. (1968) are presented in Table I-5. Table I-6 summarizes results from Mohagheghpour and Leone (1969). These data are in close agreement with results obtained from other immunological techniques (Cronin 1975, Cronin and Sarich 1975 in press).

Quantitative Precipitation

This technique involves the measuring the amount of precipitation when antibodies are complexed with antigen in large amounts. The actual procedure is detailed in Hafleigh and Williams (1966). In addition, immunological distance units, to be defined below, are interconvertible with per cent reaction in quantitative precipitation (where the amount of homologous precipitation serves as the standard of 100%) such that 200 - twice the percent cross reaction = immunological distance (Prager and Wilson 1971a, b). The following tables are drawn from Mohagheghpour and Leone (1969), Table 1-6, and Hafleigh and Williams (1966), Table I-8.

TABLE 1-4

A summary of antigenic distances taken from Goodman and Lasker (1974). Genera have been grouped starting with the smallest antigenic distances and then going to more inclusive groupings.

		Average Antigenic Distance
Homo	vs. *Pan*, *Gorilla*	0.80
Homo, *Pan*, *Gorilla*	vs. *Pongo*	1.60
Homo, *Pan*, *Gorilla*, *Pongo*	vs. Hylobatinae	2.23
Hominoidea	vs. Cercopithecoidea	3.47
Catarrhini	vs. Platyrrhini	6.49
Anthropoidea	vs. *Tarsius*	9.16
Haplorrhini	vs. Strepsirhini	10.80
Haplorrhini, Strepssirhini	vs. Tupaiaoidea	11.46
Primates	vs. Other Eutheria	12.11-14.91
Eutheria	vs. Marsupiala	15.83

TABLE I-5

Percentage cross reactivity of several nonhuman primate proteins compared with the corresponding human proteins (Wang et al. 1968).

SPECIES	Tf	M	gG	gA	gM	K	L
Homo sapiens	100	100	100	100	100	100	100
Pan troglodytes	100	98	90	100	90	100	76
Gorilla gorilla	100	100	91	100	28	100	89
Pongo pygmaens	90	100	78	100	29	95	70
Hylobates sp.	90	81	60	99	6	87	70
Macaca nigra	64	96	97	100	72	75	37
Macaca radiata	71	97	-	89	63	89	36
Macaca nemestrina	74	97	88	93	78	79	41
Macaca speciosa	65	99	87	96	81	77	37
Macaca mulatta	70	71	95	92	50	64	36
Papio sp.	69	96	99	95	76	79	40
Cercopithecus aethiops	51	79	82	89	46	61	41
Cercocebus fuliginosus	73	96	95	93	79	81	39
Crythrocebus patas	71	82	93	85	43	66	45
Callicebus sp.	22	20					
Cebus capucinus	46	29					
Saimiri sculrea	40	22					
Aotus trivigatus	29	48					
Lagothrix sp.	31	64					
Saguinus oldipus	26	23					
Lemur fulous	11	66	82				

TABLE 1-6

Immunological correspondence of Primates as determined by densitometric measurement of immunodiffusion tests and by using antisera against proteins from human serum. (Mohagheghpour and Leone 1969).

	Antisera							
Genus	A	G	H	C	gM	gG	T	Gc
Homo	100	100	100	100	100	100	100	100
Pan	94	62	70	89	74	71	80	87
Hylobates	83	59	64	80	58	53	74	70
Presbytis	81	38	45	54	56	50	56	54
Macaca	75	45	37	70	57	46	53	54
Cercopithecus	74	41	42	73	56	41	63	55
Theropithecus	76	28	40	74	56	47	52	58
Ateles	57	24	40	12	48	0	46	45
Saimiri	56	0	33	26	32	0	48	36
Cebus	63	0	33	27	23	0	42	40
Galago	48	0	28	9	21	0	0	0
Nycticebus	47	0	21	5	22	0	0	0
Tupaia	43	0	20	0	0	0	0	28

A = anti albumin, g = anti immune globulin, H = anti Haptoglobin 2-1, c = anti ceruloplasmin, gM = anti gamma M globulin, gG = anti gamma G globulin, T = anti transferrin, Gc = anti group specific component.

TABLE I-6 (continued)

SPECIES	Tf	M	gG	gA	gM	K	L
Nycticebus coucang	11	17	70	94	9	22	9
Galago senegalensis	4	4	20	82	12	23	12

Tf = anti transferrin, M = anti alpha 2 macroglobulin gG = anti gama G globulin, gA = anti gamma A globulin, gM = anti gamma M globulin, K = anti Kappa chain, L = anti lambda chain.

TABLE I-7

Immunological correspondence of Primates as determined by tusbidimetric precipin tests and by using antisera against proteins from Human serum (Mohagheghpour and Leone 1969).

Genus	Ceruloplasmin	Haptoglobin 2-1	Albumin		Globulin	
	W.C.A.	W.C.A.	W.C.A.	OP[2]	W.C.A.	OP
Homo	100	100	100	100	100	100
Pan	45	58	90	97	78	84
Hylobates	34	47	77	90	58	67
Presbytis	28	39	73	83	51	65
Macaca	22	32	67	80	47	49
Cercopithecus	29	52	60	72	45	55
Theropithecus	24	38	63	73	43	53
Ateles	20	37	53	63	17	15
Saimiri	18	36	63	68	20	16
Cebus	15	17	52	60	23	20
Galago	14	26	48	51	14	12
Nycticebus	13	23	39	44	12	10
Tupaia	11	14	31	41	3	3

1 - Whole curve area (W.C.A.)

2 - Optimal proportions zone (O.P.)

TABLE 1-8

Immunochemical correspondence values of primate serum albumins based on quantitative precipitation techniques. (Hafleigh and Williams 1966).

	% cross section
Homo sapiens	100
Gorilla gorilla	92
Pan troglodytes	97
Hylobates lar	79
Macaca mulatta	82
Colobus polylomos	78
Papio dozuera	75
Cercocebus galeritus	79
Erythocebus patas	76
Cercopithecus aethiops	79
Aotus trivirgatus	74
Ateles paniscus	58
Saimiri sciurea	60
Tamarin Tamarin	54
Lagothrix lagotricha	61
Cebus apella	45
Lemur fulous colluris	37
Lemur macaco	34
Lemur fulous fulous	37
Tupaia glis	31
Perodicticus potto	31
Galago crassicauclautus	28
Propithecus verrauriхi	22

Micro complement Fixation

Micro complement fixation (MC F) is an immunological procedure designed to measure the degree of difference between the same macromolecule from two different species. This degree of difference between two macromolecules is usually expressed in Immunological distance units (I.D.). But, the actual differences are in terms of amino acid sequence differences. The exact amount of amino acid differences between two molecules is unknown in every specific comparison. However, it is thought that one I.D. unit is roughly equivalent to one amino acid difference in either albumin or transferrin, and the general agreement between I.D. units as measured by MC'F and per cent sequence difference is quite good. Prager (Prager and Wilson, 1971 a, b) has shown a direct relationship between percent sequence difference and the immunological distance as measured by microcomplement fixation the relationship being $y = 5x$ where y = distance expressed as microcomplement fixation units and x = percent sequence difference. Immunological distance (I.D.) can be defined as 100 log I.D. I.D. is the index of dissimilarity (Wilson et al., 1964; Sarich, 1968). This is defined as the degree to which the antiserum concentration must be increased when reacted with the heterologous antigen to give the same amount of complement fixed as the homologous antigen with the antiserum. The equation for determining this distance measurement is:

$$\log \text{I.D.} = \frac{YH - Yh}{m} + \log \frac{xH}{xH}$$

where m = slope; YH = %c fixed at the peak of the homologous curve; Yh = %c fixed at peak height in the heterologous curve; xH = antiserum concentration for homologous curve; and xh = antiserum concentration in the heterologous curve (Champion *et al*., 1974).

It is a property of the complement fixation system that after a certain amount of molecular difference accumulates between the homologous molecule and the heterologous molecule, the antiserum concentrations must be increased in order to give equivalent amounts of fixation. For example, anti *Pan troglodytes* Tf has a titer of 1/10,000. That is, 75% of the complement in solution is fixed when anti *Pan* Tf is reacted with either *Pan* serum or purified transferrin at this antiserum concentration. If *Homo sapiens* Tf is reacted with this antiserum at a concentration of 1/10,000 a peak of only 40% complement fixation is attained. This suggests that changes have accumulated along both the human and chimp lineage, or that one has changed relative to the other, since both last shared a common ancestor. It is necessary to increase the antiserum concentration to 1/7400 to reach 75% fixation giving an index of 1.35 or an immunological distance of 13. If transferrins from *Theropithecus gelada* and *Aotus trivirgatus* are reacted with the anti *Pan* antisera there is no fixation at 1/10,0000. One has to raise the concentrations to 1/3880 (ID - 2.58) for *T*. *gelada* and to 1/1940 (ID = 5.15) for for *Aotus* to reach 75% fixation. These correspond to immunological distances of 41 and 71 (Figure 1-2).

Quite a few studies using the MC'F technique have been employed in the study of primate relationships. These include 1) serum al-

FIGURE 1-2

Analysis of micromplement fixation results using antisera to purified transferrins from Pan troglodytes reacted with the purified transferrins from Homo sapiens, Theropithecus gelada and Aotus trivigatus. Experiments were performed at the appropriate antiserum concentrations to give equivalent percent complement fixation.

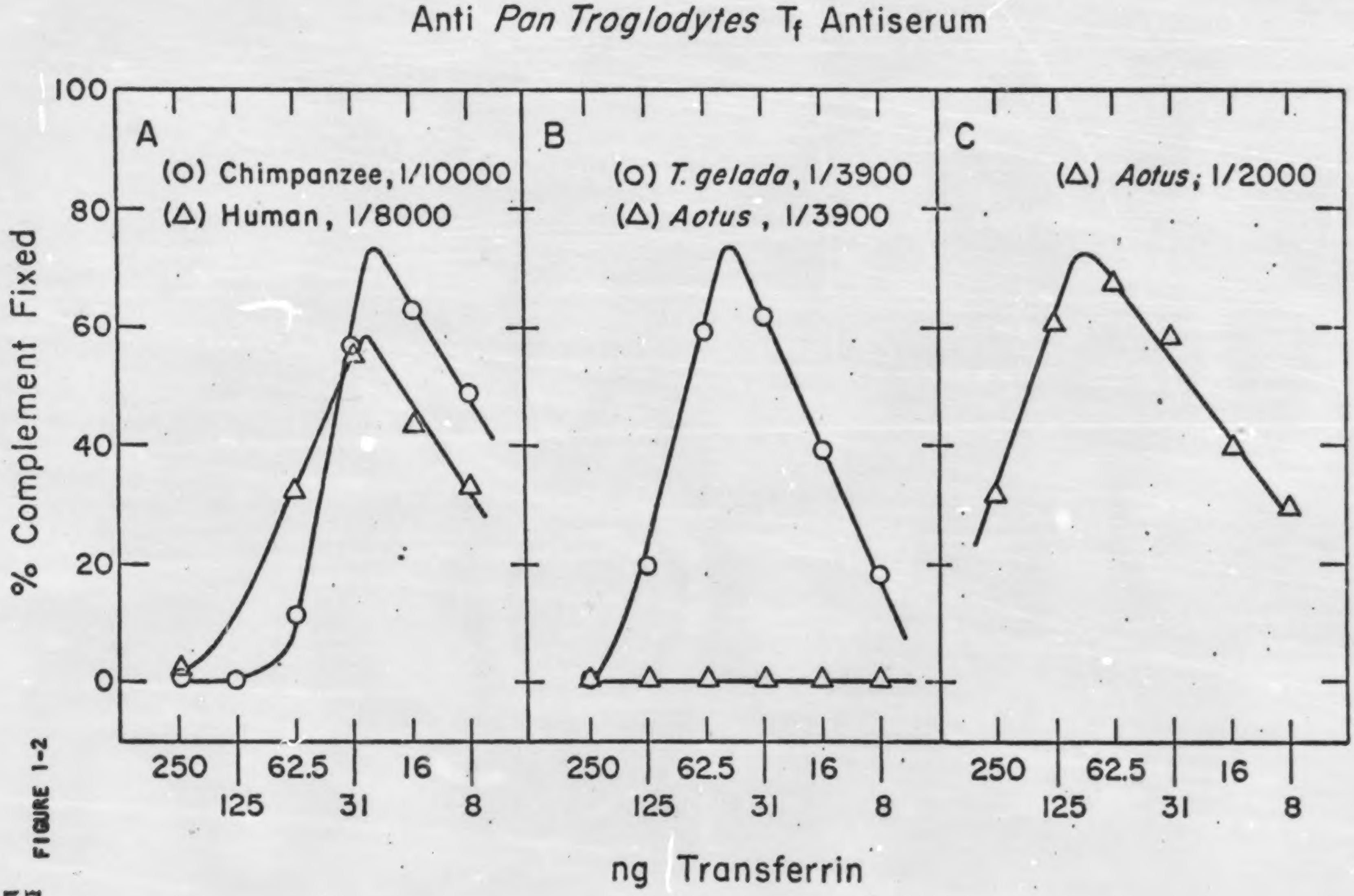

Anti *Pan Troglodytes* T_f Antiserum
% Complement Fixed
100
80
60
40
20
0
A
(O) Chimpanzee, 1/10000
(Δ) Human, 1/8000
B
(O) *T. gelada*, 1/3900
(Δ) *Aotus*, 1/3900
C
(Δ) *Aotus*, 1/2000
250
125
62.5
31
16
8
ng Transferrin

FIGURE 1-2

bumen (Sarich 1967, 1968, 1970, 1971, 1972b; Sarich and Wilson 1966, 1967a, b; Wilson and Sarich 1969; Cronin and Sarich 1975); 2) Transfeiren (Cronin and Sarich 1972, 1973a, b, 1974, 1975, Cronin and Sarich 1975; Sarich and Cronin in press); carbonic anhydrase (Nonno et al. 1969); 4) lysozyme (Hanke et al. 1973), Tables 1-9, 1-10, 1-11 are taken from Cronin 1975). Table 1-12 from Nonno et al. (1969) and Table 1-13 from Hanke et al. (1973). For more data on specific taxa refer to the papers detailed above as the data presented is merely a representative sample of the available immunological data gathered using the MC'F technique.

Several objective methods of constructing phylogenetic trees from results of protein comparisons have been published (Fitch and Margoliash, 1967; Sarich and Wilson, 1967; Sarich, 1969a; Dayhoff, 1972; Farris, 1972). These methods give rather similar results (Farris, 1972; Wallace et al., 1973; Maxson and Wilson, 1975). The method used in this study is outlined below (Cronin and Sarich, 1975 in press).

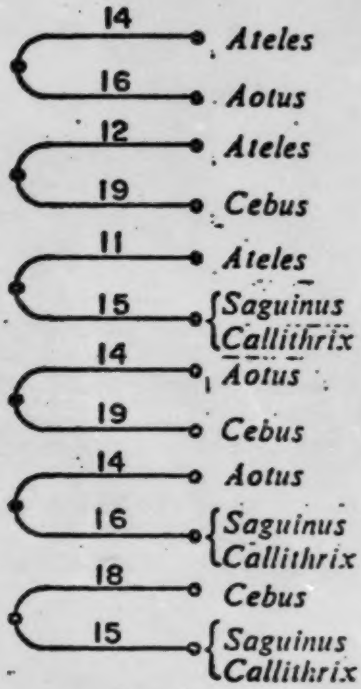
The procedure beings by using the reciprocal immunological distances from an antisera matrix. A specific example is shown in Figure 1-3. There are five antisera directed against the purified transferrins of New World monkeys: Aotus, Ateles, Cebus, Callithrix and Saguinius. The averaged immunological distance between two forms are apportioned along the two lineages by using data provided by measurements made from outside reference points. The outside reference points in this case are 11 anti-

FIGURE 1-3.

A cladistic analysis conducted with the immunological distances between the transferrins of several platyrrhine monkeys. The immunological distance matrix is given at the top left. Within the matrix, the input data is given below the diagonal. The output data, calculated from the final cladogram (lower left), is given above the diagonal. At the right of the matrix is the mean immunological distance to these platyrrhine taxa from eleven catarrhine reference points. On the right the intra platyrrhine distances are apportioned between every possible pair of taxa by the use of the eleven catarrhine reference points. The method of calculation is described in the text. The composite cladogram at the lower left is constructed from information of the lineage pair comparisons at the right. The detailed explanation of cladogram construction is found in the text.

PLATYRRHINE TRANSFERRIN ANALYSIS

	At	*Ao*	*Ce*	*Sag* *Cal*	Catarrhini
Ateles	0	29	31	28	78
Aotus	30	0	32	29	80
Cebus	31	31	0	31	86
Saguinus *Callithrix*	26	30	33	0	83


14
Ateles
16
Aotus
12
Ateles
19
Cebus
11
Ateles
15
Saguinus
Callithrix
14
Aotus
19
Cebus
14
Aotus
16
Saguinus
Callithrix
18
Cebus
15
Saguinus
Callithrix

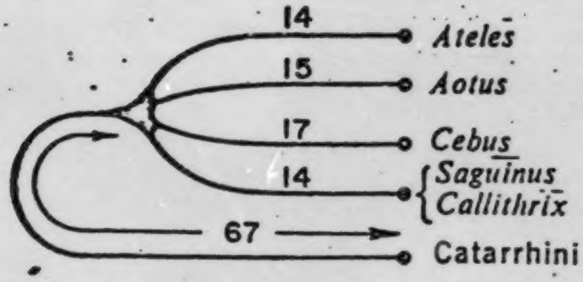

14
Ateles
15
Aotus
17
Cebus
14
Saguinus
Callithrix
67
Catarrhini

TABLE 1-9

Immunological Distances Among Primate Albumins and Transferrins[a]

	H	C	P	*Ta*	*Tu*	*Cy*	Le	Lo	Non-primates[b]	
Hominoidea	0	33	56	123	98	117	112	94	+19	
Cercopithecoidea	45	0	56	128	102	114	110	107	+19	ALBUMIN
Platyrrhini	76	91	0	109	89	98	112	107	+12	
Tarsius	172	164	156	0	93	109	122	95	+ 5	
Tupaia	170	190	180	159	0	103	117	108	- 5	
Cynocephalus	175	156	177	161	183	0	109	113	+ 5	
Lemuriformes	164	171	164	156	178	162	0	88	0	
Lorisiformes	196	195	193	178	183	185	118	0	-4	

TRANSFERRIN

---

[a] These data have been gathered using antisera to the albumins and transferrins of *Homo*, *Pan*, *Gorilla*, *Pongo*, *Hylobates*, *Papio*, *Cercocebus*, *Cercopithecus*, *Presbytis*, *Aotus*, *Ateles*, *Cebus*, *Callithrix*, *Saguinus*, *Lemur*, *Avahi*, *Lepilemur*, *Propithecus*, *Phaner*, *Daubentonia*, *Nycticebus*, *Galago*, *Tupaia*, and *Cynocephalus*; to the transferrin of *Macaca nigra*; and to the albumins of *Ursus*, *Genetta*, *Hyaena*, *Felis*, *Hipposideros*, *Pteropus*, *Tadarida*, *Antrozous*, *Bradypus*, *Cabassous*, *Tamandua*, *Scapanus*, and *Solenodon*.

[b] These numbers represent the amount by which those albumins are more (+) or less (-) distant from the various nonprimates than the lemuriform mean. A similar analysis is not possible for the transferrins as antisera to nonprimate transferrins do not generally react with those of the primates.

TABLE 1-10

Immunological Distances Among Anthropoid Transferrins[a]

	HOMO	PAN	GORILLA	PONGO	HYLOBATES	PRESBYTIS	THEROPITHECUS	PAPIO	CYNOPITHECUS	ERYTHROCEBUS	CERCOCEBUS	ATELES	AOTUS	CEBUS	CALLITHRIX	SAGUINUS
Homo	-	13	5	33	27	64	55	61	49	52	42	73	73	75	70	86
Pan	7	-	5	36	27	54	52	56	46	46	41	71	73	74	70	74
Gorilla	8	10	-	37	26	59	50	52	45	49	39	75	73	62	68	76
Pongo	16	18	24	-	28	52	50	50	42	47	38	85	83	71	74	88
Hylobates	20	22	23	35	-	55	47	45	44	45	58	78	78	82	74	85
Presbytis	34	33	37	43	43	-	20	15	19	21	21	79	89	96	90	104
Theropithecus	41	41	51	66	53	43	-	3	20	24	24	100	100	112	103	113
Papio	37	36	37	61	45	34	5	-	18	21	23	98	100	109	101	110
Cynopithecus	34	33	31	44	39	34	13	16	-	12	12	86	89	100	85	101
Erythrocebus	34	33	31	40	37	34	16	20	19	-	23	86	86	91	81	94
Cercocebus	35	28	36	39	42	31	13	20	7	9	-	82	94	89	75	92
Ateles	64	78	61	83	84	95	85	68	82	75	79	-	28	30	26	25
Aotus	67	71	60	82	80	92	89	110	77	79	81	31	-	32	35	28
Cebus	66	83	70	101	86	90	95	108	72	81	79	32	30	-	36	32
Callithrix	67	82	70	92	89	97	85	99	71	76	81	28	30	29	-	8
Saguinus	64	80	68	95	87	97	92	106	78	75	81	28	30	35	6	-

---

[a] Antisera are directed against those purified anthropoid transferrins listed in Table 1.

TABLE 1-11

Immunological Distances Among Catarrhine Albumins.

	ANTISERA									
	HOMO	PAN	GORILLA	PONGO	HYLOBATES	M. IRUS	C. AETHIOPS	PRESBYTIS	C. GALERITUS	P. PAPIO
Homo	-	4	4	11	10	37	49	42	37	34
Pan	7	-	9	11	14	37	49	46	38	31
Gorilla	5	7	-	11	10	32	62	51	37	36
Pongo	12	8	10	-	11	42	57	48	38	40
Hylobates	13	13	12	11	-	36	49	44	35	43
M. irus	37	30	21	38	36	-	12	24	6	0
C. aethiops	44	42	21	33	37	10	-	22	9	4
Presbytis	42	40	22	38	38	24	34	-	28	16
C. galeritus	39	32	20	33	33	7	0	19	-	4
P. papio	40	30	18	34	36	2	7	25	8	-

TABLE 1-12

Immunological distance units among primate carbonic anhydrases, antisera prepared against carbonic anhydrase purified from *Homo sapiens*.

Species	*Immunological Distance*
Homo sapiens	0
Pan troglodytes	4
Macaca irus	51
Macaca speciosa	52
Macaca mulatta	53
Macaca cyclopis	56
Papio papio	62
Saimiri sciurea	81
Lagothrix lagotrichia	83
Cebus capucinus	89
Tupaia glis	115
Perodicticus potto	146

TABLE I-13

Immunological differences among primate lysozymes

SPECIES	I.D. distance from human bysozyme	I.D. distance from baboon bysozyme
Homo sapiens	0	66
Pan troglodytes	0	67
Pongo pygmaeus	1	76
Gorilla gorilla	32	38
Cercopithecus aethiops	93	6
Cercopithecus talapoin	114	3
Macaca mulatta	122	1
Macaca speciosa	122	2
Papio cynocephalus	127	0
Macaca fasicularis	130	2
Macaca radiata	131	2
Saimiri scuirea	127	36
Saguinus oedipus	134	37
Callithrix jaccus	137	36
Lemur catta	151	203
Galago crassicaudatus	175	247
Lemur macaco	202	239
Lemur fulvus	212	235

catarrhine antisera (Table 1-10). For example, the Aotus-Ateles distance is 30 units, the average catarrhine-*Aotus* distance is 80 units, and the average catarrhine-*Ateles* distance is 78 units. The thirty units separating the transferrins of *Ateles* and *Aotus* should then be apportioned so that there are two more units along the *Aotus* lineage; i.e., a form further from the reference species has changed more. This procedure is repeated for every pair of taxa.

The next step is to compare one lineage, *a*, against every other lineage and then group *a* with the lineage with which *a* has the smallest distance. In this case, *Saguinus* and *Callithrix* are the closest pair. They differ by 7 units. From any other New World monkey to either is an average of 30 units. *Saguinus* and *Callithrix* can be treated as a subset or a cluster. A cluster exists when from the node that unites the taxa in question the immunological distances that separate any taxa within the subset are less than to any other form. The immunological distances from the forms involved in the cluster to every other form are averaged. This subset can then be treated as a single lineage *a'*; and tested sequentially with every other remaining lineage and joined with that lineage (i.e. *C*) to which the distance is the least.

For example, suppose *a* and *b* differ by 8 units while *a* and *b* each differ by 16 from *c* and there is no difference in rates as measured from the outside reference points. There are three pairs of taxa compared. Separating *a* and *b* are 4 units on each lineage. Similarly along the lineages separating *a* and *c* and *b* and *c* are 8 units. *A* and *b* are the closest pair and can be treated as a subset relative to *c*. The single lineage composed of *a* and *b*, *a*', has a length which is the average of the lengths as determined by the outside reference points in the *a* versus *c* and *b* versus *c* comparison. The *c* lineage is the average of the two comparisons of *a* versus *c* and *b* versus *c* also. The lineage length that unites *a* and *b* before their divergence into their separate lineages can be calculated by subtracting the averaged *a* and *b* lineage length separating the two as determined from the outside reference points, 4 units, from the total *a*' lineage length. The total a' lineage is 8 units and thus the common lineage is 4 units long. The *c* lineage is 8 units. The addition of the remaining lineages proceeds in a stepwise fashion with *a*, *b*, and *c* (*a*' and *c*) treated as a single averaged lineage *a*'. This new composite lineage is tested against every other lineage and joined with the next closest lineage untill all lineages are placed relative to one another.

In Figure I-3, *Saguinius* and *Callithrix* represent *a* and *b*. Their average lineage length from their divergence is 4 units, while their common lineage *a*' is 14. That portion of the lineage which occurs after the divergence of any other form to the divergence of *Saguinus* and *Callithrix* is thus 10 units.

In practice, the analysis is usually simplified as subsets are sometimes immediately apparent in the data. When this is observed the distances to other forms from forms within the subset are averaged and the subset becomes a single lineage. For example, there are 15 antisera to cercopithecoid transferrins (Cronin 1975). There are thus 15 separate lineages. However, they form readily definable subsets and the 15 independent lineages can be collapsed into six composite lineages. This process of collapsing the data into readily apparent major lineages precedes the cladistic analysis detailed above. Upon subsequent analysis the subsets can be broken up into their own clade.

4. Protein sequences

Techniques exist that allow the specific sequence of amino acids in a polypeptide chain to be determined. Some data is now available for primates. These include fibrinopeptides (Doolittle et al. 1971, Wooding et al., 1972 hemoglobins (Matsuda et al., 1973a, b, c; Goodman et al. 1973, 1974; Boyer et al. 1971, DeJong 1971a, b), and myoglobin (Romero-Herrera et al., 1973, 1974). For a brief summary of the protein sequence data available from primates see Goodman and Lasker (1973).

A number of different techniques for conversion of the protein sequence data into a phylogenetic tree have been published. (Fitch and Margoliash 1967; Dayhoff 1972; Farris

1972; Goodman _et al_. 1971, 1973, 1974; Goodman 1973). All give somewhat similar results.

Fitch and Margoliash (1967) have presented an elegantly simple method. First, a matrix of amino acid differences is tabulated for all species pairs. Arbitrarily the closest two species, say _a_ and _b_, are chosen as the starting point for tree construction. These two species are considered a subset and the distances, in terms of amino acid differences, are averaged to every other species. The two subset lineages are aligned through use of the average distances of _a_ to every other species and _b_ to every other species such as is detailed in the DNA tree construction section. Similar simultaneous equations are set up and using these average distances lineage lengths _a_ and _b_ can be determined. The next closest lineage is added by similar methods until all lineages are added to the tree. Arbitrarily the next closest species pair are chosen and the whole process begins again. This is repeated a number of times and the best tree is chosen. The best tree is defined as the one where the % standard deviation is lowest. This is where the output data, the distances as calculated along the branches of the constructed cladogram, deviates least from the actual measured input data. Fitch and Margoliash employed this method in constructing a cladogram of sequences from 20 cytochrome c's. Recently Goodman and others (Goodman _et al_., 1971, 1973, 1974) have developed a more refined measure of converting amino acid sequence difference to minimum mutational distance (MM)) for each pair of sequences. The calculation employs a conversion table based on the genetic code to determine at each position the minimum number of nucleotides that would need to be replaced or changed in order to convert a codon for one amino acid into a codon for another.

A computer program has been developed comparing both sequences of living species and sequences of constructed ancestral sequences of common ancestors at tree nodes. The best estimation of the correct phylogeny is the tree which overall has the minimum number of mutations. This method has been called by Goodman the maximum parsimony method. The procedure seeks that tree, of the amino acid sequences of living species, with the maximum number of codon identifies due to inheritance from common ancestors. Goodman feels that such trees are theoretically best because it seems more probable that the identities in codon sequences are due to common inheritance. The program selects the solution which minimizes the number of times a mutation is counted among lineages between the most ancestral point on the tree and each contemporary species. The mutational distance between any two species along the branches is the maximum parsimony distance (MPD). For a detailed account of this procedure see Goodman _et al_. (1973, 1974).

The following tables present the actual amino acid differences found for specific sequence comparisons. Table I-14 is from Wooding and Doolittle (1972). Table I-15, and I-16 are from Goodman and Lasker (1973). Table I-17 is from Romero-Herrera _et al_. (1973, 1974).

TABLE 1-14

Minimum numbers of amino acid replacements and base substitutions separating fibrinopeptides A and B of twelve primates (Wooding and Doolittle, 1972). Amino acid differences are below the diagonal and minimum base substitutions are above the diagonal.

	Slow loris	Cebus	Spider	Drill	Green	Rhesus	Gibbon	Siamang	Orang	Gorilla	Chimp	Human
Slow loris	-	17	17	21	18	20	16	16	17	19	19	19
Cebus monkey	15	-	3	11	8	11	8	7	8	10	10	10
Spider monkey	15	3	-	13	10	13	8	8	9	10	10	10
Drill	21	11	12	-	3	6	7	5	6	8	8	8
Green monkey	18	8	9	3	-	3	4	2	3	5	5	5
Rhesus monkey	19	11	11	6	3	-	6	5	6	6	6	6
Gibbon	16	8	8	7	4	-	-	2	3	5	5	5
Siamang	16	7	7	5	2	2	-	-	1	3	3	3
Orang	17	8	8	6	3	3	1	-	-	2	2	2
Gorilla	18	10	9	8	5	5	3	2	-	-	0	0
Chimp	18	10	9	8	5	5	3	2	0	-	-	0
Human	18	10	9	8	5	5	3	2	0	0	-	-

TABLE I-15

Amino acid differences of haemoglobin alpha chains within primates. (Goodman and Lasker, 1973).

	Man	Chimp	Gorilla	Lan	Mac	Gal	Slow	Lem	Sif	Tree
Man	0									
Chimp	0	0								
Gorilla	1	1	0							
Langur	3	3	4	0						
Macaque	4	4	5	5	0					
Galago	13	13	12	13	12	0				
Slow loris	9	9	8	10	11	8	0			
Lemur	15	15	16	15	16	16	14	0		
Sifaka	19	19	20	20	19	21	19	13	0	
Tree shrew	24	24	25	24	21	24	22	25	26	0

TABLE I-16

Amino acid differences of haemoglobin beta chains within primates (Goodman and Lasker, 1973).

	Man	Chimp	Gor	Gib	Lan	Mac	Mar	Nig	Spi	Squ	Slo
Man	0										
Chimp	0	0									
Gorilla	1	1	0								
Gibbon	3	3	4	0							
Langur	4	4	5	4	0						
Macaque	8	8	7	9	5	0					
Marmoset	7	7	8	7	5	7	0				
Night monkey	7	7	8	7	3	8	4	0			
Spider monkey	6	6	7	6	4	9	6	4	0		
Squirrel monkey	9	9	10	9	7	11	6	6	6	0	
Slow loris	11	11	12	10	10	12	11	11	12	12	0

TABLE 1-17

Amino acid differences between the myoglobus within primates (Romero-Herrera et al., 1973, 1974).

	Man	Chimp	Gib	Bab	Mac	Wooly	Squ	Mar	Gal	Lem	Tree
Man	0										
Chimp	1	0									
Gibbon	1	2	0								
Baboon	6	7	5	0							
Macaque	7	8	6	1	0						
Woolly Monkey	16	17	15	13	12	0					
Squirrel Monkey	17	18	16	12	12	4	0				
Marmoset	14	15	13	11	10	4	4	0			
Galago	23	24	24	22	21	21	23	23	0		
Sportive lemur	22	21	23	21	21	19	17	17	21	0	
Tree shrew	13	14	14	12	12	17	17	17	16	14	0

C. Discussion

1. PRIMATE EVOLUTION

The accumulation of evidence from macromolecules on the extent of differences among primates at the genetic level now permits a comparison of results from various methods. In the main, the macromolecular data are in agreement as to the cladistic or branching relationships of the various primates. This should not be surprising if what is being assayed by these techniques is some approximation of a "true" or "real" genetic distance. Below will be presented the various phylogenics constructed from the data presented in the previous section. Certain problems in interpretation of the data will also be dealt with. The discussion will center on 1) the overall perspective - the major lineages, 2) the anthropoidea, and 3) the Hominoidea. The major point of this section is to emphasize the fact that when taken as a whole the molecular data provide a fairly clear and consistent picture of the evolutionary relationships of the modern primates.

The Major Lineages

The ability to resolve lineages with great accuracy rests on two factors. First, and this is not always possible, there should be many separate lineages or clusters of separate lineages along a major phyletic branch. This provides the opportunity to either purify antigens and produce antisera directed to these antigens from an array of forms within the groups along the major lineage or to sequence protein from many different forms within the group. The first step in an immunological study would then be to clarify the within group analysis using the antisera prepared to both the antigens of species within the group and to antigens of species outside the group. Reciprocal measurements yield a more precise estimate of the antigenic difference between groups. These outside measurements provide different perspectives of the major lineage. Monotypic taxa with a long independent lineage along which have occurred large amounts of change and where antisera are not available, are mong the most difficult lineages to resolve. The same problem exists in protein sequence studies as it is sometimes difficult to assay all of the substitutions in a particular protein because of back mutations or because multiple hits at a specific codon remain unseen. Without, other closely related sequences to compare it is hard to know with great exactitude the "true" sequence of events that occurred along the major lineage. The more sequences avaliable the greater the chance of detecting back mutations and parallel mutations and multiple hits at a codon. Tarsius, a monotypic lineage, is an example of a form whose placement has proven difficult.

The macromolecular data in general suggest that the primates, including the anthropoidea, Lemuriformes and Lorisiformes, are a group relative to any other mammalian group. Protein sequence studies including fibrinopeptide (Wooding and Doolittle, 1972), mygoglobin (Romero-Herrera, 1973) and alpha and beta haemoglobin (Goodman et al., 1974) seem to indicate that the primates share a monophyletic lineage along which occurred a number of substitutions. Although, in some cases, involving the haemoglobins the evidence is not as clear cut as with the former two molecules.

The micro complement fixation data suggest that these primates, named above, share a fairly long common lineage along which accumulated a large number of substitution in both albumin and transferrin. There are five major lineages that can be resolved given the present immunological data. The five lineages appear to radiate from a common node and include the Anthropoidea, the common Lorisiformes-Lemuriformes lineage, and the independent branchees leading to Tarsius, Tupaia and Cynocephalus (Figure I-4). The latter two are not usually considered primates, at least taxonomically. The relevant immunological data are presented in Table I-9.

The transferrin data indicate that the Lemuriformes and Lorisiformes share a short common lineage after the divergence of the lineages leading to other primate forms. The albumin data only weakly associate the two groups with the exclusion of the other lineages. Romero-Herrera (Romero-Herrera et al., 1973) based on data from myoglobin sequences associates the two with a few substitutions occurring along a common lineage. Dene (Dene et al.) using immunodiffusion also detects this common lineage.

The case for inclusion of Tupaia, Tarsius and Cynocephalus in the clade primates, not necessarily taxonomically, is strengthened by the fact that the transferrins of these forms cross react strongly with antisera directed against the transferrins from species which are normally classified as primates. From a primate anti-transferrin perspective, only certain rodents and carnivore transferrins cross react. The latter cross reactions are extremely weak. The transferrins of no other order of mammals cross react with anti primate transferrins.

Goodman (Goodman, 1973; Goodman et al., 1974) on the basis of immunological data places Tupaia outside the primates. It is, however, the closest non primate lineage. On the basis of its myoglobin sequence Romero-Herrera (Romero-Herrera et al., 1974) cannot place Tupaia either inside or outside the clade primates. Dene et al. (manuscript, 1975) place Cynocephalus as a lineage that is outside the primates in a similar position as Tupaia. Tarsius is associated with the Anthropoidea in a taxon (semiorder) Haplorhini (Goodman, 1973; Goodman et al., 1974). At the present moment the existance of a common Tarsius and Anthropoid lineage can not be documented with the albumin and transferrin immunological data. Recent preliminary evidence on the alpha and beta haemoglobin sequences from Tarsius suggest that it is not cladistically closer to either the anthropoidea or to the remaining prosimians. It is however a primate.

The molecular data indicates that if Cynocephalus and Tupaia are not strictly cladistic primates then they would be the closest outside species to the group normally considered primate, usually the anthropoidea, Tarsius and the Lemuriformes.- Lorisiformes. It is unclear, as of yet, if any of these lineages seems slightly more closely related to any of the other lineages (except for the Lemuriformes - Lorisiformes group). There is not a strong association of any pair of these major lineages. Yet, we cannot conclude with certainty that this may not be true. Only more molecular data will clarify the problem of resolving whether these necessarily short lineages existed. From morphological consideration, McKenna (1974) has recently proposed that the order Dermoptera (Cynocephalus), Tupaioidea and Primates be grouped together in the superorder Archonta (Simpson, 1945)

Anthropoid Evolution

Given the data, it is readily apparent that the anthropoidea is composed of three clusters of species, including the Hominoidea, the Cercopithecoidea and the Ceboidea. The former are closer to each other from almost every molecular measure, except for the primate lysozyme data, than they are to the latter group the Ceboidea. Reciprocity problems are inherent in the lysozyme - anti lysozyme system as has been pointed out (Prager *et al*., 1974). The overwhelming evidence is that the Catarrhini are a unit relative to the Platyrrhini.

All the molecular data support the conclusion that the anthropoidea share a common lineage subsequent to the divergence of any prosimian stock. Along this lineage accumulated some 70 units of combined albumin and transferrin units of change, three myoglobin sequence changes, seven fibrino peptide changes, five beta haemoglobin changes and two units of antigenic distance, before the divergence of the New World monkeys.

The ceboidea form a fairly tight unit evolutionary radiation with a division into units the Callithricidae plus *Callimico* and a number of other fairly independent ceboid lineages (Cronin and Sarich, 1975, Baba *et al*., 1975, Boyer *et al*., 1971).

The Catarrhini form a group relative to the Platyrihini, with respect to serum proteins, albumin and transferrin (Sarich 1970, Sarich and Cronin 1975), prealbumin, albumin alpha   macroglobulin, thryglobulin, transferrin, ceruloplasmin and gamma globulin (Goodman *et al*., 1971), DNA (Kohne, 1972), myoglobin (Romero-Herrera, 1973), haemoglobin (Goodman *et al*., 1973, 1974), fibrinopeptides (Wooding *et al*., 1972) and carbonic anhydrase (Nonno et al., 1969).

The Catarrhini are traditionally broken into two taxonomic units, the Hominoidea and the Cercopithecoidea on morphological grounds. This is also true with respect to the molecular division (all references above and figures this paper). The Cercopithecoidea have had little detailed genetic work. Yet it is apparent that the basic division into leaf eaters (Colobinae) and non leaf eaters (Cercopithicine) is recognized at the molecular level. (Sarich 1970, Banicot and Wade 1970, Goodman and Moore 1971). A detailed presentation of the evolution of the Cercopithecoidea as determined by the Micro complement fixation technique is in preparation (Cronin and Sarich) and a brief preliminary version is in press (Sarich and Cronin, 1975).

Hominoid Evolution

The Hominoidea are similar to each other in amino acid sequences of haemoglobins, myoglobin, fibrinopeptides, carbonic anhydrases, and DNA. The immunological data also make it apparent that the Hominoidea is a tight knit group. Traditional taxonomy has divided the Hominoidea into three groups separated from each other, usually at the family level, the Pongidae (sometimes including the subfamily Hylobatinae) the Hominidae, and the Hylobatidae, if not included in Pongidae.

The immunological and sequence data, as well as the DNA data, clearly support an early divergence of the gibbon lineage. However, a major question in Hominoid cladistics evolution is the position of Pongo, the orang, vis a vis the other lineages. MC'F studies seem to indiate that the orang diverges approximately at the same time the gibbon lineage diverges away from the lineage leading to man, chimp and gorilla.

The DNA data of Hoyer (Hoyer et al., 1972) also supports this evolutionary position of the orang. DNA data from Kohne (1972) study on the position of orang study is lacking. On the other hand, the immunodiffusion data and the fact that the orang seems to share along with man, chimp and gorilla a change in common at position 4 in fibrinopeptide A suggests that the orang may be somewhat cladistically closer to man, chimp and gorilla. Sequence data with respect to orang myoglobin or haemoglobin is lacking.

It appears that there is a common lineage leading to a three way divergence of man, chimp and gorilla subsequent to the divergence of the Hylobates and Pongo lineages. Along this lineage accumulates some 4 albumin units, transferrin units, some 2% DNA sequence change, two fibrino peptide substitutions, two carbonic anhydrase substitutions, two beta globin changes, one myoglobin change and about one unit of antigenic distance.

There appears to be no association of chimp and gorilla after the divergence of the lineage leading to man. Since the three lineages have separated they have accumulated about 4 transferrin units, 3 albumin units, 2 haemoglobin substitutions along the gorilla lineage, one myoglobin change along the chimp lineage and one haemoglobin substitution on the human lineage. No fibrinopeptide substitutions have occurred on any of the three lineages.

The DNA data is not helpful here as the studies of Kohne et al. (1972) failed to include Gorilla. In the study of Hoyeret al., (1972), Pan and Homo appear to be somewhat closer. Yet from the perspective of

Pongo the *Gorilla* DNA seems to have evolved more so that *Homo* and *Pan* may not be actually cladistically closer but may only appear so because *Gorilla* has diverged units DNA sequence more than *Homo* or *Pan*. An electrophoretic survey of *Gorilla* proteins would prove useful as would a cladistic analysis of chromosonal evolution (i.e. translocations, inversions, deletions, etc.) in *Pan*, *Homo* and *Gorilla*. In summary, all molecular evidence suggests that man, chimp and gorilla are a monophyletic lineage and that all are extremely similar at the genetic level. In fact, because of their close genetic similarity and the cladistic relationship among the African apes and man, Goodman (1962, 1963a, b) has suggested that the African apes be removed from the Pongidae and placed within the Hominidae in the subfamily Homininae (Goodman and Moore 1971).

FIGURE I-4

A phylogenetic analysis of the major primate lineages based on the albumin and transferrin immunological distances of Table II-9. The numbers above the lines indicate the number of albumin plus transferrin units of change allocated to that lineage. The bats are included as probably one of the closest groups to the primates. The time scale is drawn using the relationship of 125 units of albumin plus transferrin change per 60 million years along an average mammalian lineage.

FIGURE I-5

A transferrin cladogram of the anthropoidea constructed according to the method described in the text and in Figure II-3. The immunological distances on which this phylogeny is based are those of Table II-10. The percent standard deviation is 8.9%. The number in parenthesis following the species names represent the amount of transferrin immunological distance accumulated on that species' lineage from the node separating the catarrhines and platyrrhines.

FIGURE 1-6

A DNA cladogram of the primates constructed according to the method detailed in the text. The DNA differences on which this is based are taken from Table II-2. The numbers above the lineage represent per-cent nucleotide substitution occurring along that lineage.

FIGURE 1-7

A cladogram of the primates based on the immunodifusion data. Differences are expressed as antigenic distance units. (adapted after Goodman and Moore, 1971).

FIGURE 1-8

A fibrinopeptide cladogram of 12 primates. The numbers above the lineages represent numbers of amino acid substitutions occurring in fibrinopeptide A and B along that lineage. (Adapted after Wooding and Doolittle, 1972).

FIGURE 1-9

An alpha haemoglobin cladogram of 10 primates. The numbers above the lineages represent numbers of amino acid substitutions occurring along that lineage. The cladogram was constructed by the maximum parsimony method. (Adapted after Goodman _et al._, 1972)

87

FIGURE I-10

A beta haemoglobin cladogram of 12 primates. The numbers above the lineages represent numbers of amino acid substitutions occurring along that lineage. The cladogram was constructed by the maximum parsimony method (adapted after Goodman _et al_., 1972).

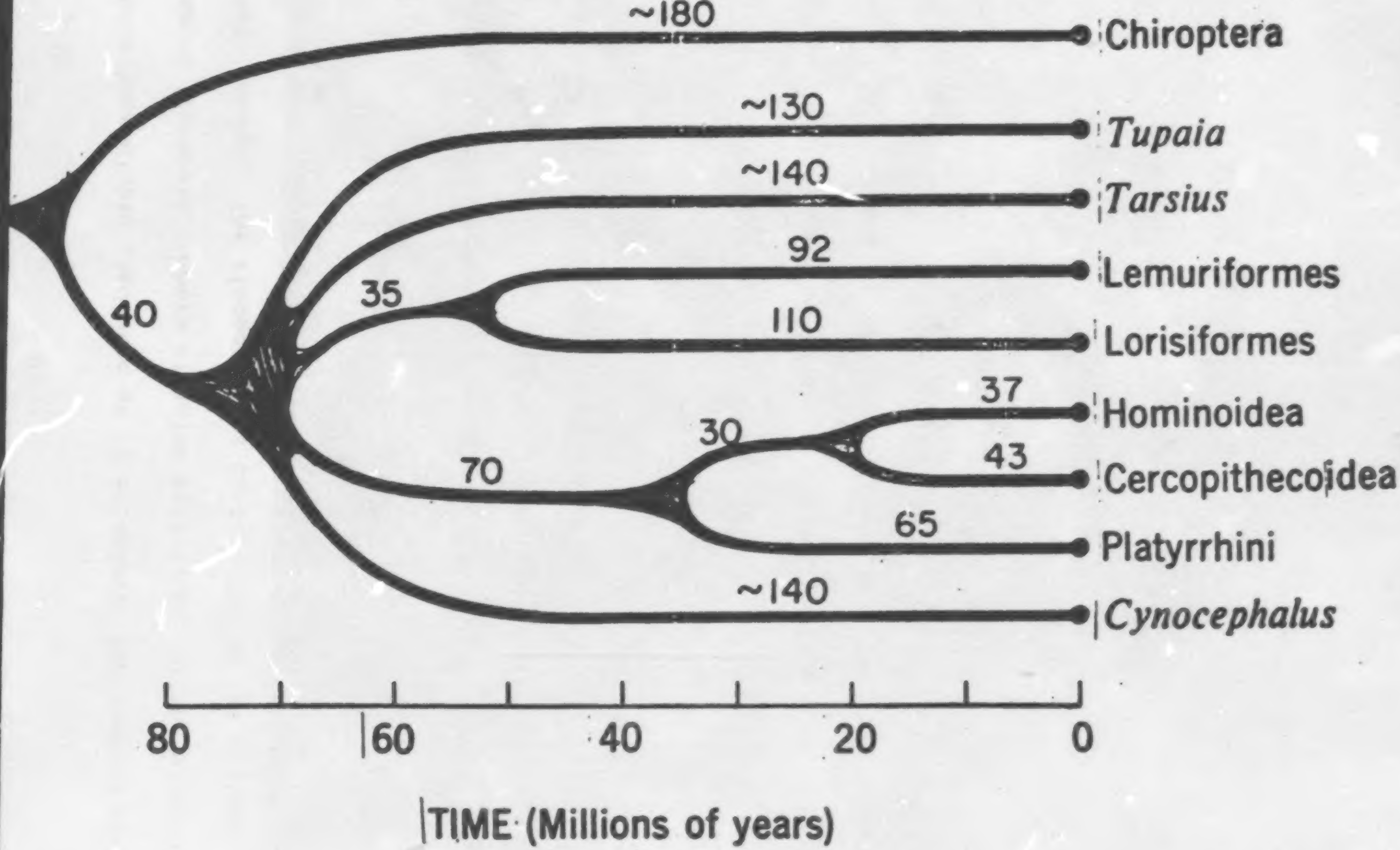
FIGURE I-11

A myoglobin cladogram of 10 primates. The numbers above the lineages represent number of amino acid substitutions occurring along that lineage. (adapted after Romero-Herrera _et al_., 1973).

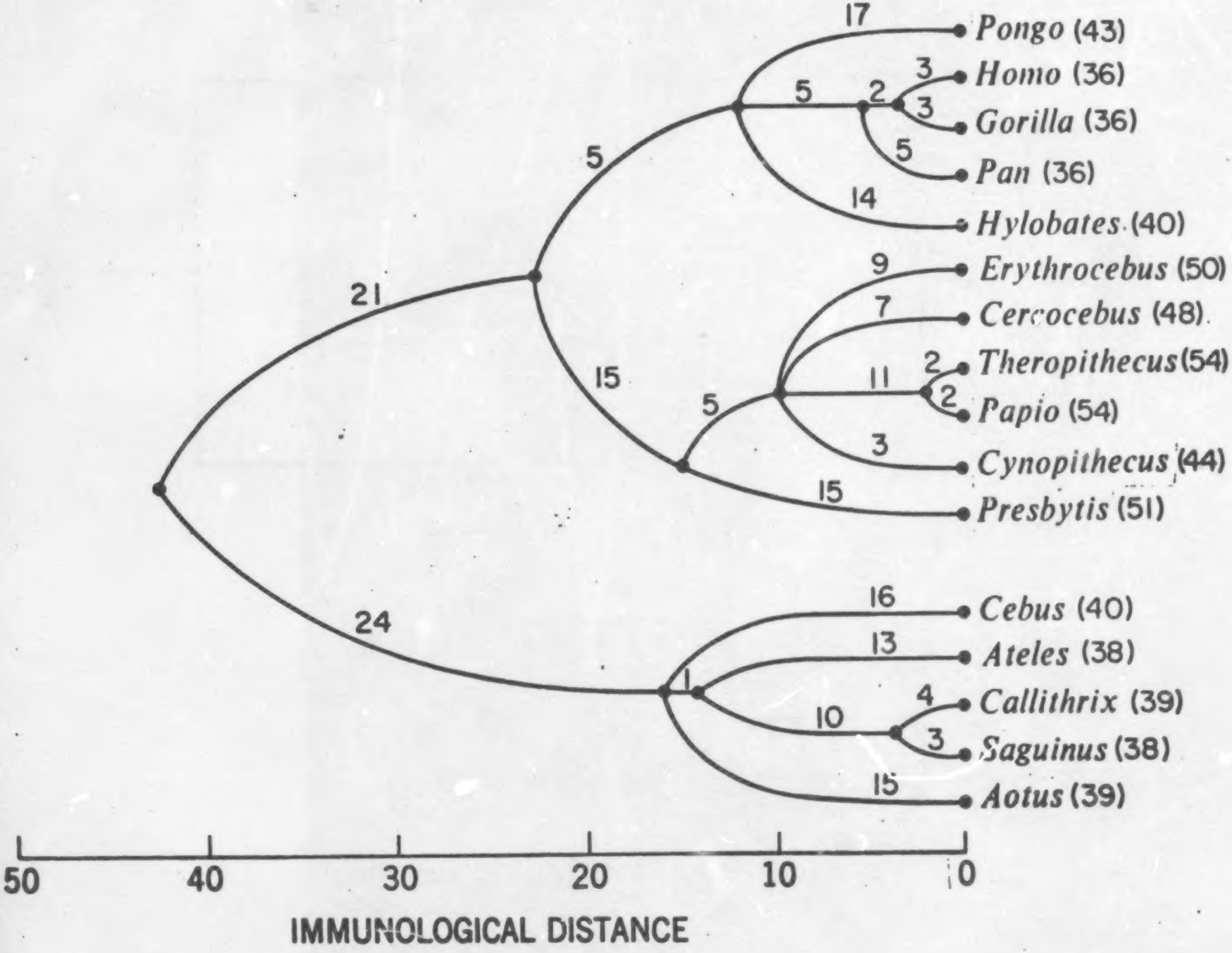
FIGURE I-12

The combined albumin, transferrin and DNA phylogeny of the Hominoidea. The numbers on the lineages are, in order, the number of albumin and transferrin units of change, and the ΔT_m times 10 for that lineage. Data is drawn from Tables II-2, II-3, II-10, II-11.

ALBUMIN PLUS TRANSFERRIN PHYLOGENY OF PRIMATES AND RELATED MAMMALS


~180
Chiroptera
~130
Tupaia
~140
Tarsius
92
Lemuriformes
35
110
Lorisiformes
40
37
Hominoidea
30
43
Cercopithecoidea
70
65
Platyrrhini
~140
Cynocephalus
80
60
40
20
0
TIME (Millions of years)

TRANSFERRIN PHYLOGENY


17
Pongo (43)
3
Homo (36)
5
2
3
Gorilla (36)
5
5
Pan (36)
14
Hylobates (40)
9
Erythrocebus (50)
21
7
Cercocebus (48)
2
Theropithecus (54)
15
11
2
5
Papio (54)
3
Cynopithecus (44)
15
Presbytis (51)
16
Cebus (40)
24
13
Ateles (38)
1
4
Callithrix (39)
10
3
Saguinus (38)
15
Aotus (39)
50
40
30
20
10
0
IMMUNOLOGICAL DISTANCE

DNA PRIMATE PHYLOGENY

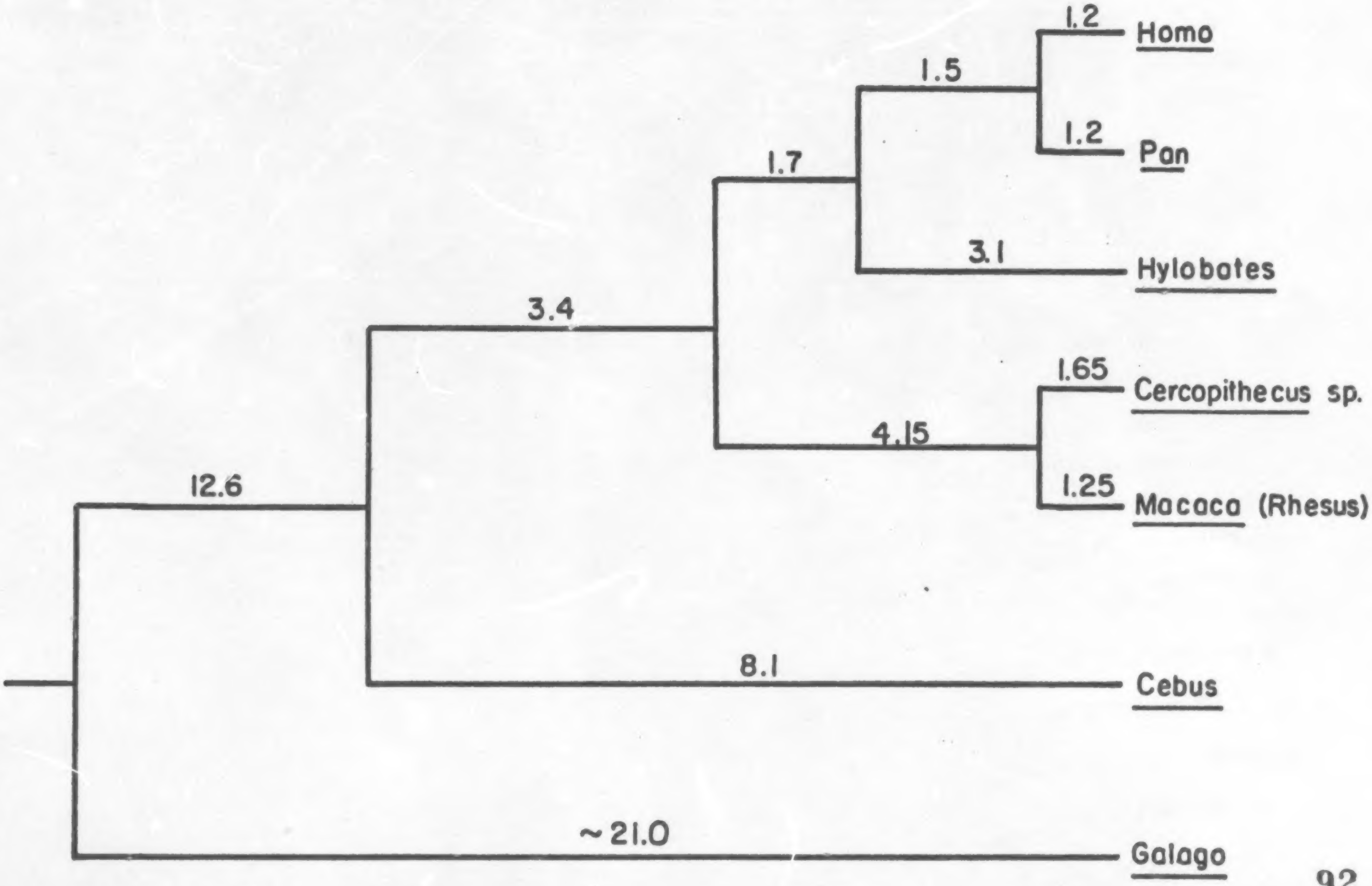

1.2
Homo
1.5
1.2
Pan
1.7
3.1
Hylobates
3.4
1.65
Cercopithecus sp.
4.15
1.25
Macaca (Rhesus)
12.6
8.1
Cebus
~21.0
Galago

FIGURE 1-6

PRIMATE IMMUNODIFFUSION PHYLOGENY

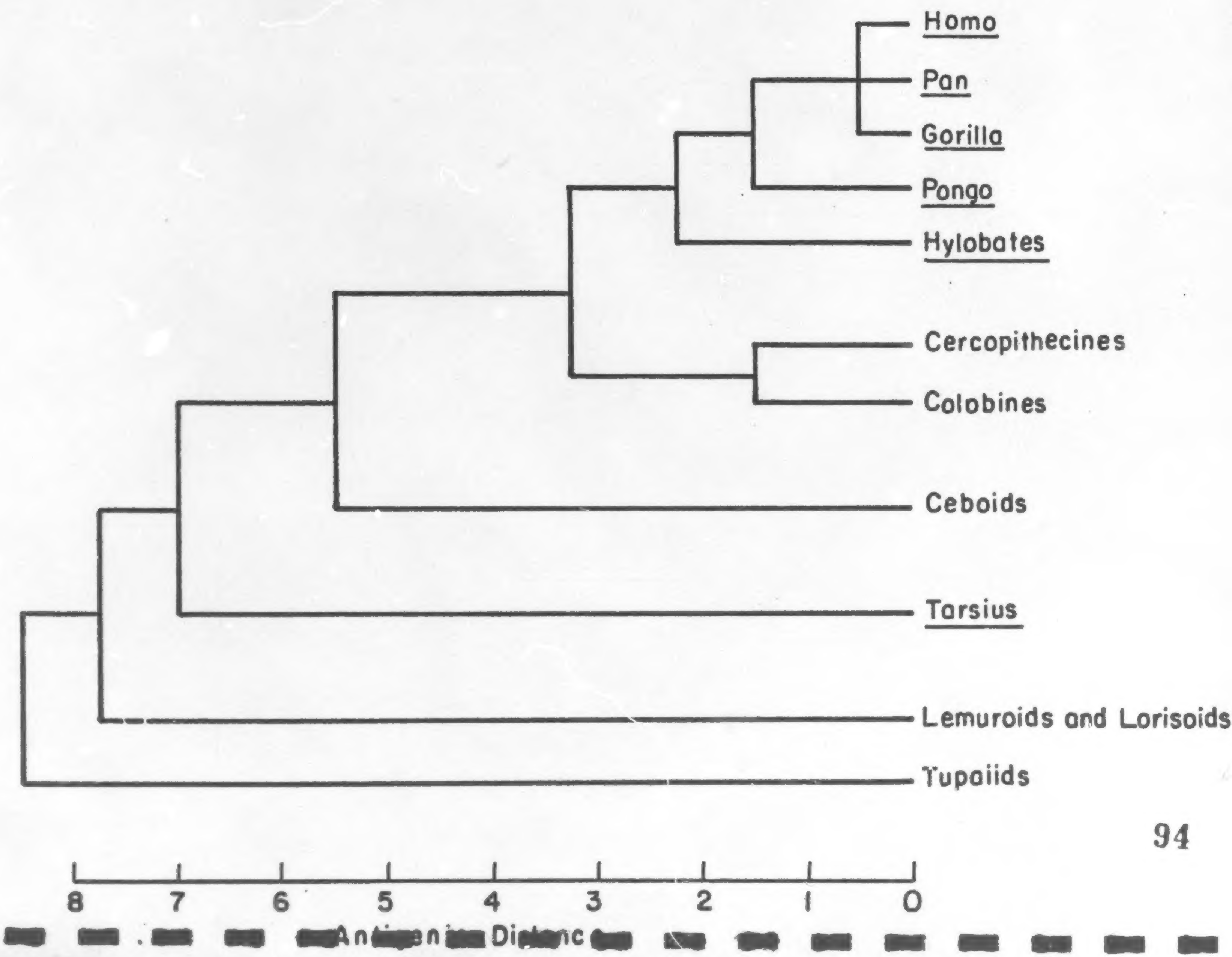
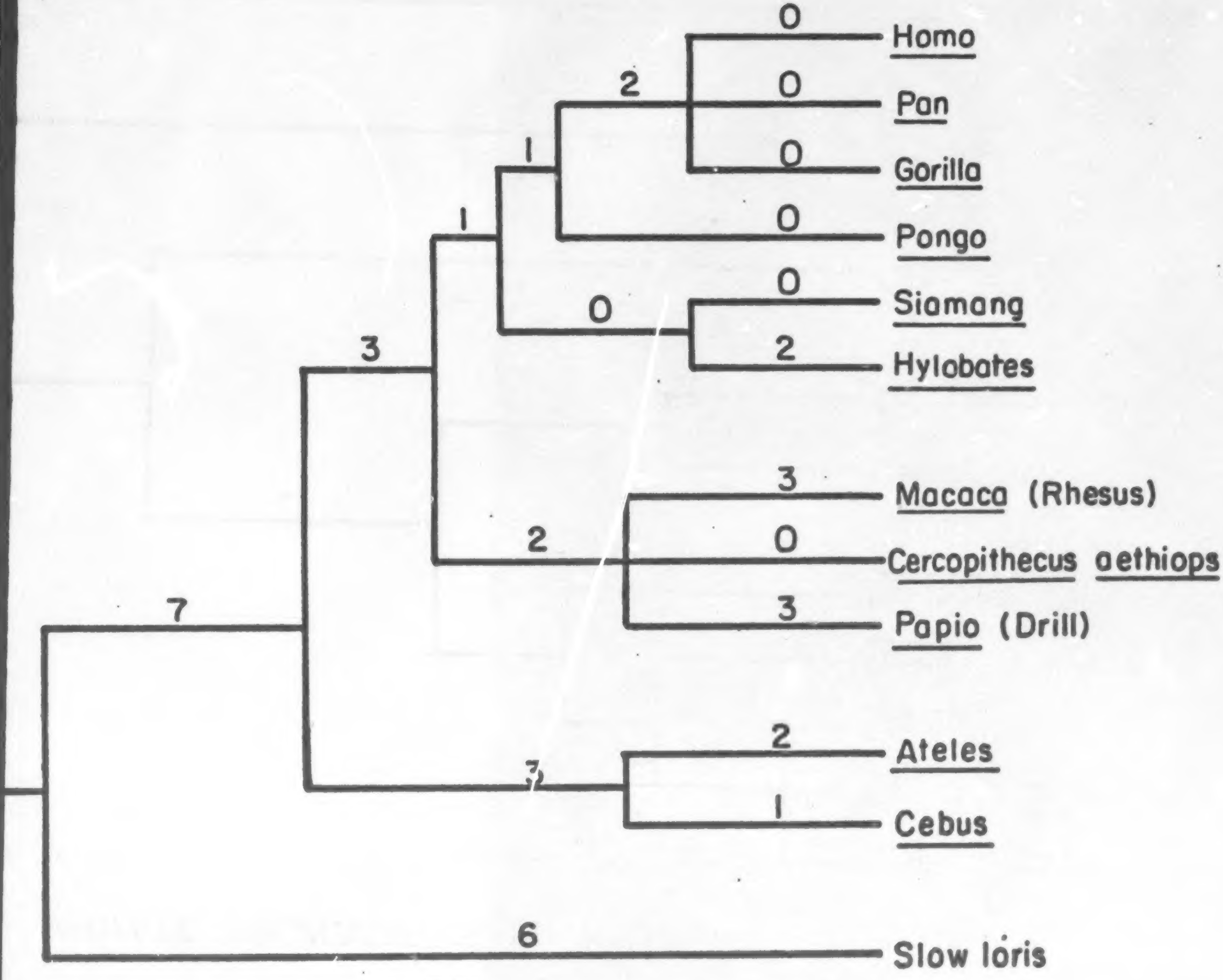

Homo
Pan
Gorilla
Pongo
Hylobates
Cercopithecines
Colobines
Ceboids
Tarsius
Lemuroids and Lorisoids
Tupaiids
8
7
6
5
4
3
2
1
0
Antigenic Distance

FIGURE 1-7

PRIMATE FIBRINOPEPTIDE (A+B) PHYLOGENY


0
Homo
2
0
Pan
1
0
Gorilla
1
0
Pongo
0
0
Siamang
3
2
Hylobates
3
Macaca (Rhesus)
2
0
Cercopithecus aethiops
7
3
Papio (Drill)
2
Ateles
3
1
Cebus
6
Slow loris

PRIMATE ALPHA HAEMOGLOBIN PHYLOGENY

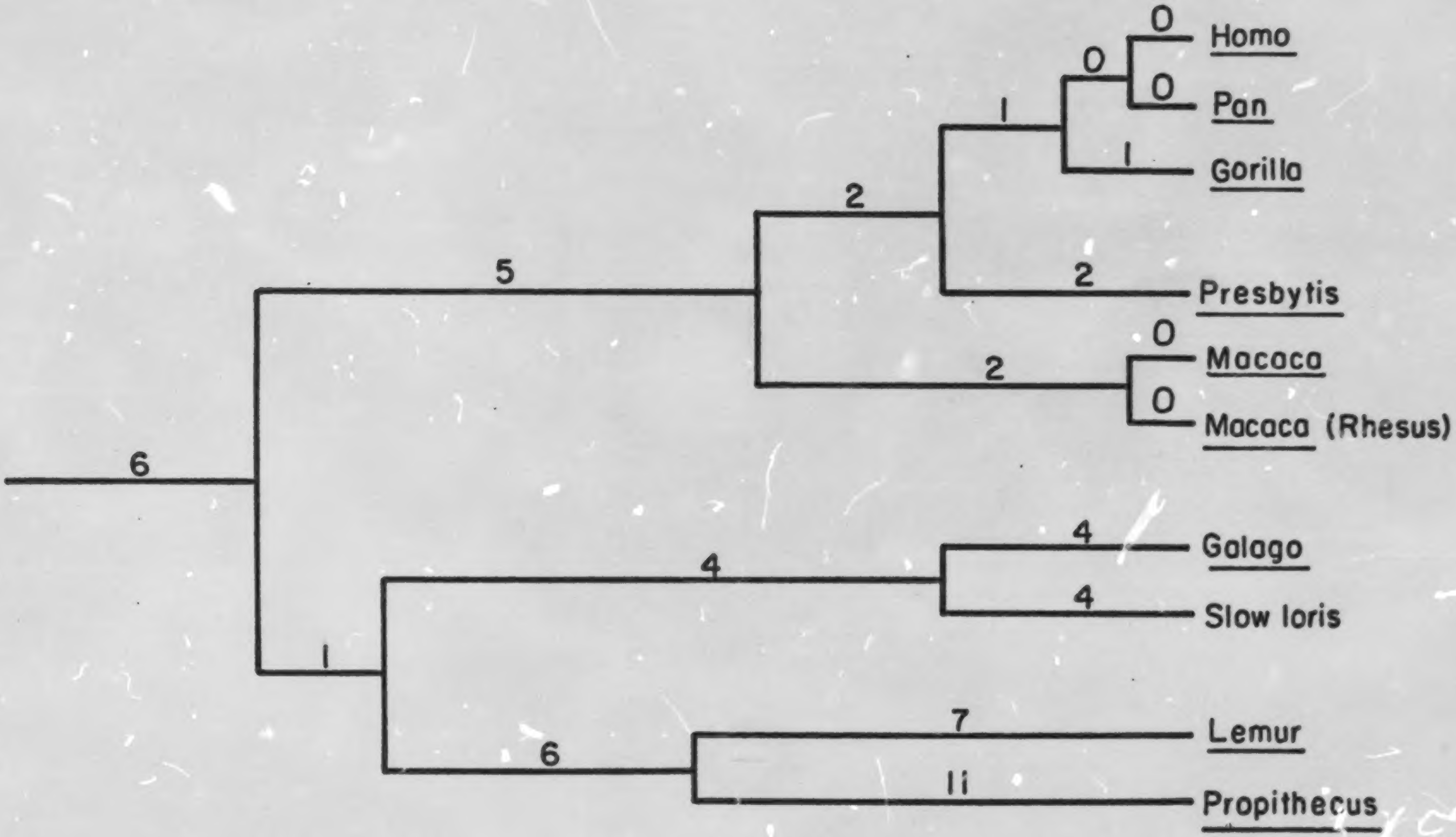

0
Homo
0
0
Pan
1
1
Gorilla
2
2
Presbytis
5
0
Macaca
2
0
Macaca (Rhesus)
6
4
Galago
4
4
Slow loris
1
7
Lemur
6
11
Propithecus

FIGURE 1-9

PRIMATE BETA HAEMOGLOBIN PHYLOGENY

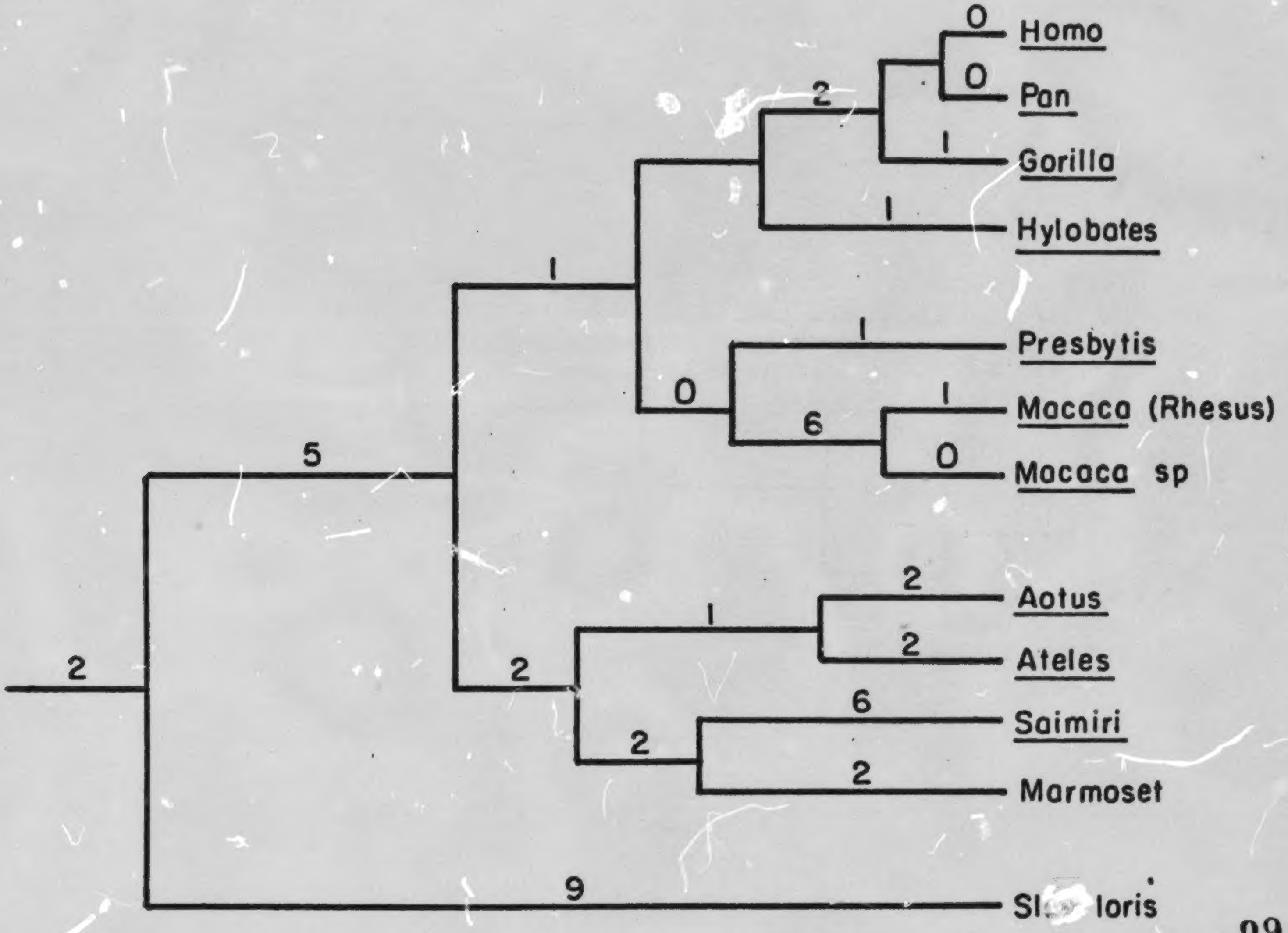

0
Homo
0
Pan
2
1
Gorilla
1
Hylobates
1
1
Presbytis
0
1
Macaca (Rhesus)
6
0
Macaca sp
5
2
Aotus
1
2
Ateles
6
Saimiri
2
2
2
Marmoset
2
9
Sl[illegible] loris

FIGURE 1-10

MYOGLOBIN PRIMATE PHYLOGENY

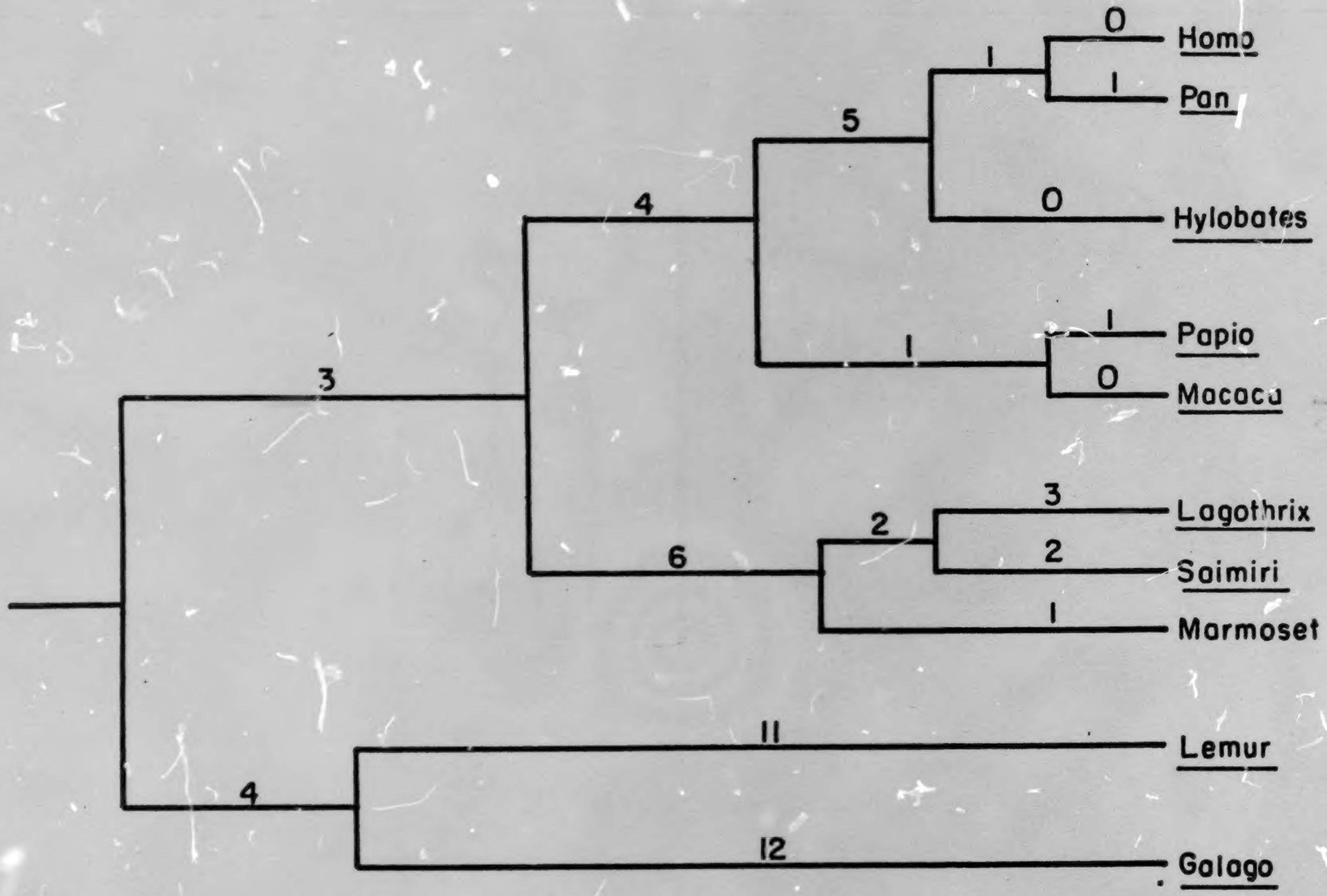
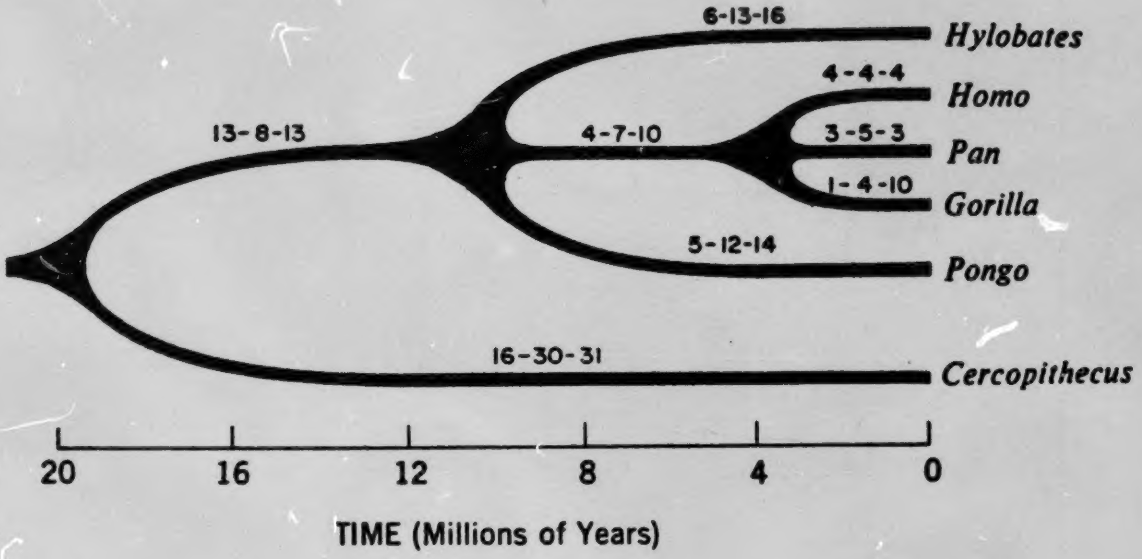

0
Homo
1
Pan
1
5
0
Hylobates
4
1
Papio
1
0
Macaca
3
3
Lagothrix
2
2
Saimiri
6
1
Marmoset
11
Lemur
4
12
Galago

FIGURE 1-11

ALBUMIN, TRANSFERRIN, AND DNA PHYLOGENY OF THE HOMINOIDEA


6-13-16
Hylobates
4-4-4
Homo
13-8-13
4-7-10
3-5-3
Pan
1-4-10
Gorilla
5-12-14
Pongo
16-30-31
Cercopithecus
20
16
12
8
4
0
TIME (Millions of Years)

2. TIME SCALE FOR PRIMATE EVOLUTION

Calibration of an Immunological Clock

It appears that albumin accumulates approximately 50 units of change per sixty million years per lineage or 100 units per sixty million years of separation. Similar results have been found for a large variety of vertebrates, carnivores (Sarich, 1969), ranid frogs (Wallace *et al*., 1973), hylid frogs (Maxson, 1973; Maxson and Wilson 1975), and iguanid lizards (Gorman *et al*., 1971).

Transferrin accumulates about 150 units per sixty million years of separation in mammalian and snake lineages (Mao *et al*., 1971; Cronin and Sarich, 1972, 1975 in press; Sarich, 1974). In birds the rate of transferrin evolution is one quarter to one half that found in mammals and snakes. Similiar results are observed in serum albumin with a rate of evolution one third that found in mammals (Prager *et al*., 1974). This phenomen of an evolutionary slowdown in birds is not unique to these two molecules. Lysozyme and cytochrome *c* seem to evolve twice as slowly in birds as in mammals (Prager et al., 1974). This problem points to the fact that rates of evolution cannot be assumed; they must be calculated for every group under study.

In the equation Immunological Distance = K x Time (10^6 year), K approximates 1.67 for albumin and 2.5 for transferrin per million years for mammalian lineages. Thus, 250 units of combined albumin plus transferrin immunological distance calibrates to approximately sixty million years. Using this calibration point for albumin and transferrin it can be seen in Table 1-17 what the times of separation of various taxa are for the two molecules independently and averaged. There is a close agreement between what either molecule alone predicts.

Table 1-18 lists the relative genetic distances between the same taxa when other molecules are compared. The molecular data when considered as a whole support the hypothesis that the immunological data is not unique or unrepresentative of such macromolecular evidence. Dates of divergence between the taxa listed are easily calculated given the data. The data in Table 1-18 correlated at the 0.96 level. A manuscript is in preparation to detail these genetic distances (Cronin, Sarich and Dempster, in pre.).

The dates of divergence calculated from the immunological data presented in this study are in good agreement with dates proposed by Sarich, 1970; Sarich and Wilson, 1967a and b; Wilson and Sarich, 1969. Certain differences are, however, apparent. It was postulated that prosimians and anthropoids differed by about 100 albumin units. This figure has had to be adjusted upwards given the addition of five new lemurid albumin antisera. A further point of difference is the date of 30 million years for the hominoid-cercopithecoid divergence used to calculate the man-chimp divergence time of 5 million years (Sarich and Wilson, 1967b).

In subsequent publications a divergence time of approximately 22 million years has been estimated for the hominoid-cercopithecoid separation (Sarich, 1970, 1971). The date estimated by transferrin of 18 million years is in close agreement with this latter figure.

TABLE 1-17

Times of Divergence Among Various Primate Taxa Predicted by Albumin and Transferrin Immunological Distances

Taxa	Time of Divergence (10^6 yrs.)[a]		
	Albumin	Transferrin	Average
Homo vs *Pan* vs *Gorilla*[b]	3.6	4	3.8
Homo vs *Pongo* vs *Hylobates*[b]	7.2	9.6	8.4
Colobinae vs Cercopithecinae	14.4	10.8	12.6
Hominoidea vs Cercopithecoidea	22.2	18	20.1
Platyrrhini vs Catarrhini	34.2	33.6	33.9
Anthropoidea vs Prosimii	70.2	64	67.1

[a] Times of divergence are calculated on the basis that approximately 100 albumin and 150 transferrin units accumulate between two taxa over sixty million years.

[b] The taxa listed are cladistically equally divergent from a common node so that it is a three way comparison. Since all three lineages separated cladistically from the same node, they have existed for equal evolutionary time.

TABLE 1-18

Relative Molecular Differences Among Various Primate Groups Referred to a Catarrhine-Platyrrhine Distance of 1.0

Groups Compared	Albumin[a]	Transferrin[b]	DNA[c]	Mixed Immunology[d]	Myoglobin[e]	Fibrinopeptides[f]	Beta Haemoglobin[i]	Carbonic Anhydrase[j]	Lysozyme[k]
Homo vs Pan	0.12	0.13	0.15	0.12	0.08	0	0	.05	0
Homo vs Pongo vs Hylobates[g]	0.25	0.30	0.33	0.29	NA[h]	0.3	.43	NA	NA
Hominoidea vs Cercopithecoidea	0.38	0.53	0.61	0.53	0.5	0.5	.85	.65	.90
Catarrhini vs Platyrrhini	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Anthropoidea vs Prosimii	2.1	1.8	2.6	1.67	1.5	1.8	1.57	1.73	1.45

[a] From Sarich (1970) and subsequent work in this laboratory. The number is immunological distance between the groups divided by the catarrhine-platyrrhine albumin immunological distance.

[b] Data from this laboratory and expressed as in a.

[c] Calculated from the data in Hoyer et al. (1972) and Kohne, Chiscon, and Hoyer (1972) by dividing the ΔT_m for the groups by the corresponding catarrhine-platyrrhine value.

[d] From Goodman and Lasker (1973).

[e] From Romero Herrera and Lehmann (1973). The calculations are based on amino acid differences.

[f] From Wooding and Doolittle (1972; Tables 1 and 2). The calculations are based on amino acid differences

[g] The taxa listed are cladistically equally divergent from a common node so that it is a three-way comparison.

[h] The amino acid sequence of Pongo myoglobin is unknown.

[i] From Goodman and Lasker (1973). The data presented is based on amino acid differences found between the taxa.

[j] From Nonno et al. (1969).

[k] From Hanke et al. (1973; Table 11). Only the data gathered with the anti human lysozyme is included.

This earlier publication (Sarich and Wilson, 1967b) assumed a hominoid-cercopithecoid divergence time of approximately 30 million years. From this date, given the ratio of the man-chimp albumin distance of 6-7 units, versus the hominoid-cercopithecoid distance of 35 ID units, and given the hypothesis of the regularity of protein evolution a time of divergence of 5 million years was calculated for man and chimpanzee. Additional albumin data have now been gathered. Given the 10 x 10 albumin catarrhine matrix (Table II-11) a mean hominoid-cercopithecoid distance of 37 immunological distance units is obtained. A cladistic analysis of the hominoids indicates that man, chimp, and gorilla diverged from a common node into three separate lineages. Each lineage is a sample of the amount of change given that time of divergence for those lineages. A mean distance using all descendent lineages from a node may give a better representation of the actual distance between species descending from that node than only one measurement. This consideration gives a mean man-chimp-gorilla albumin distance of 6 units. The same analysis on the transferrin data reveals a mean man-chimp-gorilla immunological distance of 8. The hominoid-cercopithecoid mean is 45 transferrin units. The ratio is 1:6.1 for albumin and 1:5.6 for transferrin. Given the small distances involved between the great apes and man, the two ratios are consistent and predict that the human-chimpanzee divergence is somewhat less than four million years.

Objections to the Immunological Clock

Objections to the immunological clock usually stem from two sources. The first are objections based on the fact that the time scale of divergences of certain taxa seem to be at variance with certain interpretations of the fossil record. The second class of objections stem from a belief that either there is no basis for a clock, that is evolutionary rates are not constant, or that molecular evolution in certain lineages has decelerrated. This slowdown can either be caused by a correlation of molecular evolution with generation length (shorter generation - faster rate of evolution or vice-versa) or by certain physiological selective constraints. The main objectives to an immunological clock will be dealt with briefly below. These objections have been answered in the literature.

Table 1-19 and Figure 1-14 are an adaptation from various sources presented by Simons (1969, 1972). Similar objections have been expressed by others (Uzzell and Pilbeam, 1971; Leakey, 1970). Simons, as can be seen in Figure 1-14, objects both at the cladistic level and the temporal level to the phylogenies presented in Figures 1-4 and 1-15. Figure 1-15 is adapted from Sarich (1970) and is shown first for a historical perspective and, secondly to show how the addition of the transferrin data has clarified and resolved certain problem areas.

Some object to the molecular clock based purely on paleontological consideration. For example, Simons believes that certain fossil forms are ancestral to specific living hominoids, including the following associations, 1) Ramapithecus - Homo, 2) Dryopithecus africanus - Pan, 3) Dryopithecus major - Gorilla and, 4) Pliopithecus and Limnopithecus - Hylobates. Ramapithecus dates to about 14 million years from the Miocene of East Africa. If this form is ancestral to Homo, then the divergence of the Hominidae and Pongidae occurred much before the 4-5 million years predicted by the immunological clock. Similarly if D. africanus and D. major are ancestral to chimp and gorilla and date to 15-20 million years ago then the Pan-Gorilla divergence is minimally early - Mid Miocene again much greater than the immunological clock would suggest. Similarly, the gibbon divergence is dated to perhaps 30-35 million years ago. The Hominoid-Cercopithecoid split would be about 45 million and the Catarrhini-Platyrrhini divergence around 55 million. A rebuttal to each specific interpretation is not in order here. Yet, others from a morphological viewpoint have objected to the assignments of these forms to the lineages Simons has proposed (Morbeck, 1972; Andres and Waller, 1976).

Some authors believe that the cladistics are correct but the clock is not accurate for various reasons. They believe that the molecular picture can be brought into accord with certain interpretationsof the fossil record by recognizing that rates of molecular evolution are dependent on either generation length or upon the complexity of placentation. For example, Kohne (Kohne et al., 1972) has suggested that the close genetic relationship of man and chimp has been due to a slowdown in the rate of genomic evolution in higher primates, not due to recent divergence times. Kohne et al., (1972) and Lovejoy et al., (1973) have postulated that generation length affects the rate of evolution. If mutations are primarily limited to DNA replication, then the number of replications occurring from germ line to gamete decreases per unit time as generation length increases. By assuming specific divergence dates for various taxa Kohn, Table I-21 , calculates that the rate of nucleotide substitution since divergence of two lineages has decreased in higher primates because of increasing generation length compared to lower primates and short generation form mammals. Lovejoy has suggested (Lovejoy _et al_., 1973) that if these genetic distances are corrected by a generation length factor then times of separation of various taxa can be brought into accord with estimates of divergence times based on the fossil record. Similarly Bauer (1973), Table I-20 sees in immunodiffusion data times of divergence of taxa more in accord with proposed paleontological derived dates. Goodman, again assuming specific divergence times for various taxa, has suggested a slowdown in higher primates rate of evolution. The causative mechanism would be selection against transplacental immunization (Goodman 1962, 1963a, b; Goodman _et al_., 1971, 1972). Table I-22 presents the sequence data interpreted in this manner.

Sarich and Wilson, (1973) and Sarich (1972, 1973) have specifically dealt with the question of a slowdown in higher primate evolution. They suggest that the hypothesis of a slowdown is directly testable. They report that the amount of albumin evolution in higher primates is the same as in lower primates when lineages are measured from reference points outside the primates, Table I-23 . Short generation forms do not seem to accumulate more changes in albumin than do longer generation forms which is what the generation time model would predict. The amount of evolution occurring in the mouse lineage compared to that occurring in the man or chimp lineage is the same. Yet, the generation times differ and have differed since the divergence of the mouse and human lineage by a significant amount (Sarich 1974).

Furthermore, they suggest that the DNA data and the sequence data can be interpreted to suggest that the rate of evolution of these molecules are linearly related to time. For example, if you suggest that the human chimp DNA difference accumulated in 5 M.Y. then ask how long it took for the DNA differences to accumulate between other taxa, then the dates calculated agree extremely well with the immunologically predicted times. This would be true for every molecule in Table I-18 . Because, the ratios of the genetic differences agree so well then predicted divergence the dates would agree.

It may be noted that the times of divergence of the various taxa within the primates are assumed. If you initially assume a long temporal separation between man and chimp, and the genetic distance is small, than it might be logical, if not inevitable, to conclude that there has been a slow rate of evolution along the two lineages. However, the assumption of divergence dates especially when a few million years is a significant proportion of the total lineage length, in order to prove there has been a slowdown in molecular evolution in higher primates may be a circular argument. (Sarich (1974) suggests that the phenomenon of a slowdown has never been demonstrated to have any existence independent of certain interpretations of the primate fossil record. Sarich reports that the concept of using molecules as a molecular clock is confirmed by direct testing of the clock hypothesis itself.

Two further criticims of the molecular clock method have been put forward. These have both been answered in depth by Sarich (Sarich 1974).

Read and Lestrel (1970) have suggested that a log-log model of the index of the dissimilarity vs. time is a better fit to the paleontological data than the semi log model. Sarich (1974) has countered this by noting the non predictive nature of the log-log model and the fact the log-log model contradicts known capabilities in terms of the power of discrimination at the amino acid level, of the micro complement fixation technique. Furthermore, direct immunological tests of avian lysozymes of known sequence suggests that the semi log model gives an excellent fit to the data, Prager and Wilson (1971a, b).

Uzzell and Pilbeam (1971) have suggested that the rate test as employed in MC'F to measure rates of evolution is insensitive. They suggest that as two species are separated for longer and longer periods of time the actual difference in terms of sequence differences grows faster than the measured difference due to back mutations parallel substitutions and multiple substitutions at the same codon. Since MC'F measures amino acid differences the method underestimates genetic distances by ever increasing amounts. So if you set your clock on a genetic distance, at one end of the scale which is an underestimation of the actual genetic distance then on the recent end of the scale, the genetic distances measured actually took less time to accumulate than the calculations would suggest.

Sarich (1974) presents data to counter this argument. He states that the MC'F technique, even at the end of the range of distances measureable by the technique, can discriminate between the amount of evolution that occurred along the Aotus compared to the Cebus lineage.

Aotus is some 20 units more conservative, less evolved, than the Cebus lineage. If there is a significant phenetic underestimation of the time phyletic genetic distance, then the further removed you are in an evolutionary sense (i.e., antibodies made to albumin from species further and further away evolutionarily) then the more this 20 unit difference would disappear. Because as you move away the less discrimination you expect because of multiple hits, parallel substitutions, etc. However, this is not the case. Hominoid reference antisera detect this 20 units as do prosimian anti albumin as well as anti carnivore albumin. The latter immunological distances approach the operational limit of the MC'F technique. Thus, it is probably that the degree of phenetic underestimation of phyletic distance is relatively unimportant over the range of immunological distance, from 0-40% sequence difference, where the MC''F technique is operational. This is also suggested by the work of Prager and Wilson (1971a, b) where there is a linear relationship of amino acid differences vs. immunological distance, ranging from 0-40% sequence difference. Antibody recognition of homology terminates at approximately 40% sequence difference. Most objections have been answered in print and for a more detailed account of these answers to specific objections raised to the molecular clock hypothesis, as applied to primates, see Sarich (1972b, 1974) and Sarich and Wilson (1973).

TABLE I-19

Divergence dates of various primate taxa based on an interpretation of the fossil record. (Adapted after Simons 1969, 1972).

TAXA	Time of divergence x 10^6 years
Homonid-Pongid	~ 20-25
Pan-*Gorilla*	18-20
Pongidae-Hylobatidae	> 30
Hominoid-Cercopithecoid	~ 45
Catarrhini-Platyrrhini	~ 55
Prosimii - Anthropodea	60-70

TABLE I-20

Times of divergence of various primate taxa based on a linear model of immunological relevant accepted mutation between species vs. time. Based on 28 different plasma proteins using immunodiffusion experiments. (Bauer 1973).

	Relative time units	Absolute [illegible] 10[illegible] years
Homo	100	0.0
Pan	86.2	9.7
Gorilla	82.6	12.1
Pongo	77.5	15.7
Cercocebus	62.1	26.5
Macaca	61.0	27.3
Cercopithecus	58.0	29.4
Erythrocebus	57.3	29.9
Cebus	22.9	54.9
Galago	9.5	63.3
Eutheria	0.0	70.0

Time of divergence based on an assumption of a Eutherian Primate divergence of 70 million years ago.

TABLE 1-21

Rate of nucleotide substitution calculated in terms of absolute time. (Kohne et al., 1972)

DNA's compared	Millions of years of divergence	Total divergence time	% nucleotide substitutions since divergence	% change per 10^6 years	Nucleotide pair changes per year
Man-Man	0	0	0	0	0
Man-chimp	15	30	2.4	0.08	1.6
Man-gibbon	30	60	5.3	0.09	1.8
Man-green monkey (G.M.)	45	90	9.5	0.1	2
Man-capucin	65	130	15.8	0.12	2.4
Man-galago	80	160	42	0.26	5.2
GM-GM	0	0	0	0	0
GM-rhesus	15	30	3.5	0.12	2.4
GM-man	45	90	9.6	0.11	2.2
GM-chimp	45	90	9.6	0.11	2.2
GM-gibbon	45	90	9.6	0.11	2.2
GM-capucin	65	130	16.5	0.12	2.4
GM-galago	80	160	42	0.25	5.0

TABLE 1-22

Rates of substitutions of nucleotides in alpha and beta haemoglobin and fibrinopeptides in the time period of the origin of the eutheriacs to gorilla, chimpanzee and man (Goodman _et_ _al_., 1972)

Time period in 10^6 years	alpha haemoglobin # of nucleotide replacements	alpha haemoglobin Rate 10^6 yrs.	beta haemoglobin # of nucleotide replacements	beta haemoglobin Rate 10^6 yrs.	fibrinopetide A + B # of nucleotide replacements	fibrinopetide A + B Rate 10^6 years
90-65'	12	1 per 2	11	1 per 2	9 or 6	1 per 3 or 4
65-40	7	1 per 3.5	6	1 per 4	4	1 per 6
40-15	1	1 per 25	4	1 per 6	3	1 per 8
15 - gorilla, chimp, man	1,0,0	1 per 45	1,0,0	1 per 45	0,0,0	1 per 45

'Estimates of divergence times based upon interpretations from the fossil record. [Eutherian radiation 90 M.Y.; Primate radiation 65 MYBP; Hominoid-Cercopithecoid 40 M.Y.B.P.; Man-chimp-gorilla divergence 15 M.Y.B.P. (M.Y.B.P. = millions of years before present)]

TABLE I-23

These tests for the occurrence of an evolutionary slowdown in the hominoid lineage. (Sarich and Wilson, 1973)

A. MC'F test with antisera to the albumins of four carnivore species.

Species	Mean I.D.
Homo sapiens	162
Macaca mulatta	166
Ateles geoffroyi	149
Nycticebus concang	125
Lemur fulvus	135
Tarsius spectrum	137
Tupaia glis	156

B. Precipitin test with antiserums to the albumins of seven nonprimate species.

Species	Mean I.D.
Homo sapiens	169
Hylobates lar	169
Macaca mulatta	169
Aotus trivigatus	1[illegible]0
Cebus capucinus	169
Nycticebus concang	143
Lemur fulous	150
Tupaia glis	163

TABLE 1-23 (continued)

C. Mc'F test with antiserums to the albumens of five New World monkey species.

Species	Mean I.D.
Homo sapiens	55
Hylobates lar	53
Macaca mulatta	53
Presbytis entellus	52

FIGURE 1-13

A phylogeny of the primates based on the evolution of the serum protein albumin. This phylogeny may be compared with Figure II-4 where additional data has been added and resolving power increased. For example, a common Lemunformes - Lorisiformes lineage is apparent with the addition of the transferrin data. Similarly, additional albumin and transferrin data suggest the orang (Pongo) lineage is part of a three way divergence, one lineage leading to Hylobates, and the second the common Pan, Gorilla, Homo lineage and the third the orang lineage. Thus, Pongo is not associated with the latter lineage subsequent to the gibbon's divergence as the earlier data suggested. (adapted after Sarich, 1970).

FIGURE 1-14

A phylogeny of the primates based on an analysis of the fossil record. Boxes with enclosed numerals along lineages indicate that a specific form is associated with that lineage at the approximate time so indicated by the numerals within the box. For example, on the lineage leading to Homo the boxed number 14 represents the form Ramapithecus dated to 14 million years ago, from East Africa. This form has been considered by some to be ancestral to Homo. (adapted after Simons, 1969, 1922).

PRIMATE ALBUMIN PHYLOGENY

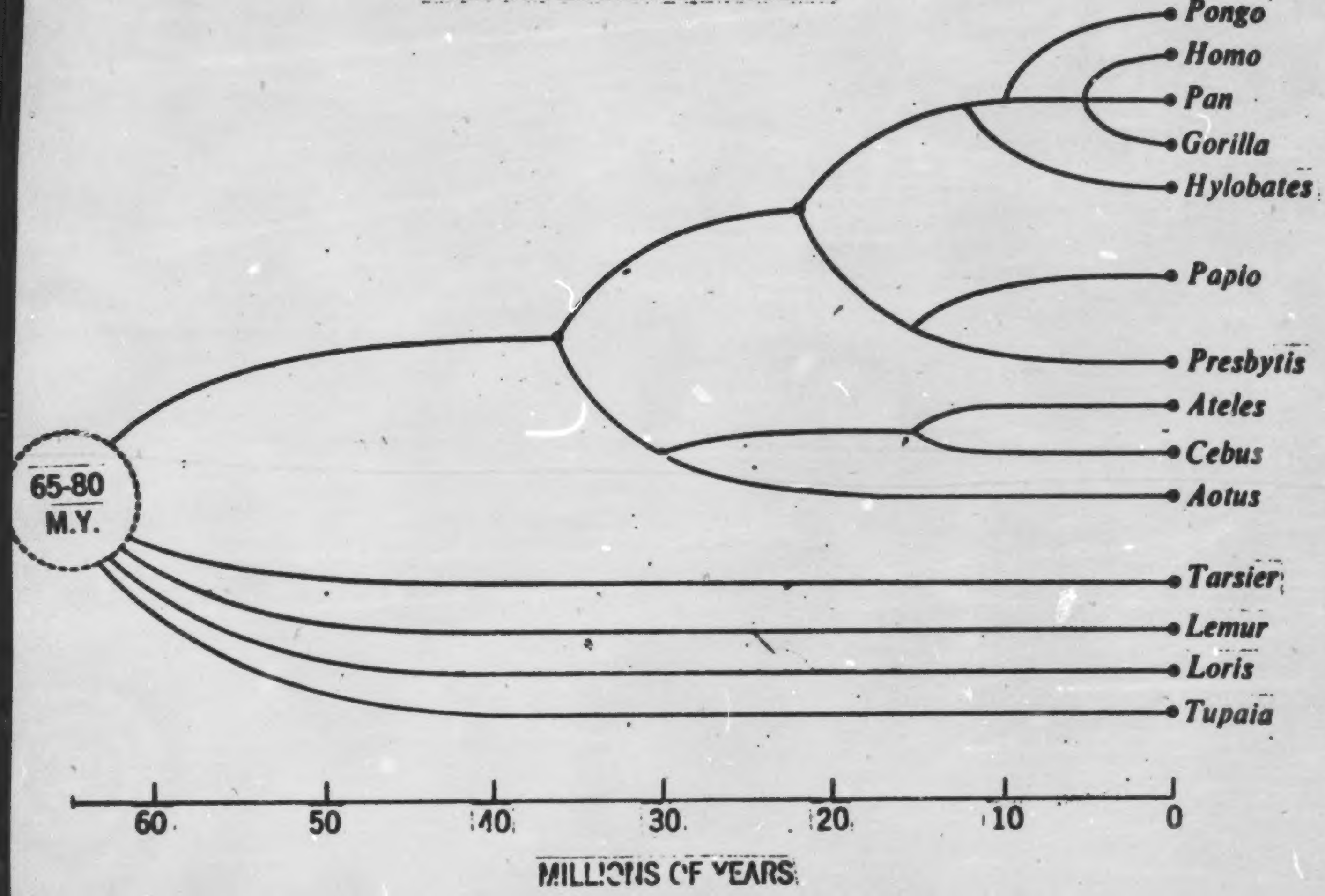
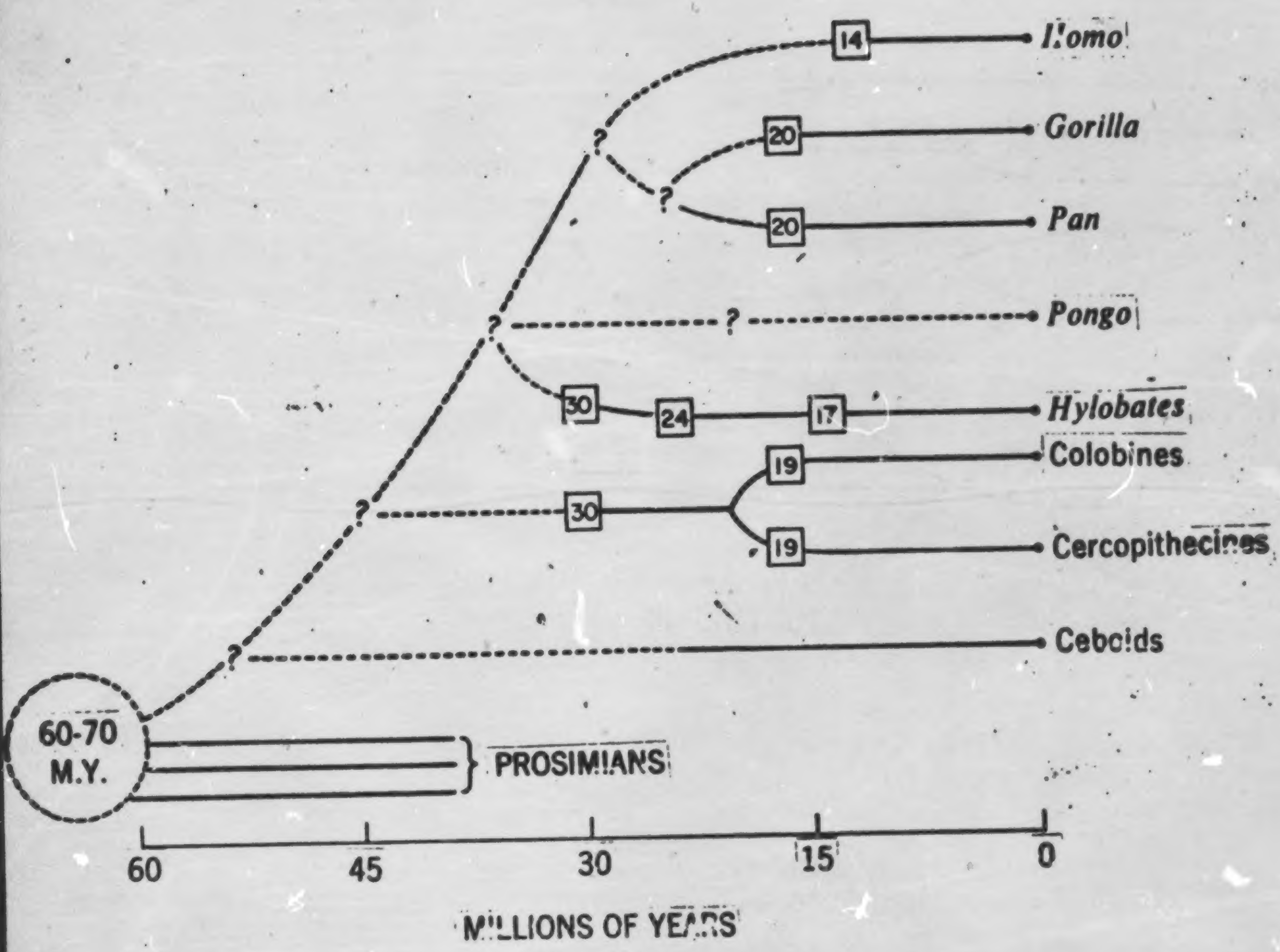

Pongo
Homo
Pan
Gorilla
Hylobates
Papio
Presbytis
Ateles
Cebus
Aotus
Tarsier
Lemur
Loris
Tupaia
65-80
M.Y.
60
50
40
30
20
10
0
MILLIONS OF YEARS

FIGURE 1-14


Homo
Gorilla
Pan
Pongo
Hylobates
Colobines
Cercopithecines
Cebcids
PROSIMIANS
60-70 M.Y.
14
20
20
30
24
17
19
30
19
?
60
45
30
15
0
MILLIONS OF YEARS

3. Macromolecular Evidence Bearing on the Question of the Man-African Ape Divergence Time

The question of the ape-human divergence time is one of the most controversial of points. It has been known for some years how close the genetic relationships is between apes and humans (Goodman, 1961, 1962, 1969a and b; Hafleigh and Williams, 1966).

Recent molecular work has confirmed earlier observation that man and apes are extremely closely related at the genetic level. These data include information from DNA studies, globin sequences, fibrinopeptide sequences, mixed immunology, and electrophoretic studies. Besides cladistic information, these data can yield estimates of the time of divergence of humans and apes.

King and Wilson (1975) have surveyed proteins encoded by 44 loci using electrophoretic comparisons. The genetic distance between human and chimpanzees is a very small one and on the order of the genetic distance found between sibling species of Drosophila or mammals. They further estimate that the average human polypeptide is more than 99% identical to its chimpanzee homologue. In fact, the probability that human and chimp alleles are electrophoretically identical is 0.52. This genetic distance yields an estimate of a time of divergence of humans and chimps on the order of 4-8 million years (King, 1973), Table 1-24.

Sequences of fibrinopeptides are available now for twelve primates, including the five hominoid genera (Wooding et al., 1972). The sequences of fibrinopeptides A and B, a total of thirty resides, are identical for human, chimp, and gorilla. It is possible to calculate an average rate of substitutions found within the primates for the fibrinopeptides. All anthropoids must be equally separated in time from Nycticebus. Since these two taxa separated there has been an average of 17 substitutions separating any anthropoid and Nycticebus. If it is assumed that prosimians and anthropoids separated approximately 70 million years ago then this works out to approximately one substitution per 4 million years. A separation time between human and chimp of 15 million years or 30 million years total between the two forms would predict that the two forms would differ by some 7 substitutions. A direct ratio comparison of the genetic distance between Homo and Hylobates using the catarrhine-platyrrhine separation as a reference point indicates that Homo and Hylobates are .3 or 30% of the catarrhine-platyrrhine distance (Table 1-18). If we use a calibration point of 35 million years for the reference point then Homo and Hylobates separated about 10.5 million years ago. (This is in agreement with the immunologically predicted date.) Since two mutations have occurred along the common Homo, Pan, Gorilla lineage this lineage must represent some time depth. Given the fact that the great apes and man do not differ in these sequences a range of 0 to 10.5 million years is indicated for the best estimate of the times of divergence.

The analysis of information from hemoglobin sequences may proceed in a similar fashion. An extensive number of alpha, beta, gamma and delta chain hemoglobin sequences are available from various species of

TABLE 1-24

Differences in amino acid sequences of human and chimpanzee polypeptides. The proteins with the postcript (1) have been compared immunologically the remainder by direct amino acid sequencing.

Protein		Amino acid differences	Amino acid sites
Fibrinopeptides A and B		0	30
Cytochrome e		0	104
Lysozyme[1]		~ 0	130
Haemoglobin (alpha)		0	141
Haemoglobin (beta)		0	146
Haemoglobin (A gamma)		0	146
Haemoglobin (G gamma)		0	146
Haemoglobin (delta)		1	146
Myoglobin		1	153
Carbonic anhydrase[1]		~3	264
Serum albumin[1]		~6	580
Transfearin[1]		~8	647
	TOTAL	~19	2633

adapted after King and Wilson (1975).

primates (Goodman _et al_., 1971; Boyer _et al_., 1971). Man differs from chimp in only one amino acid substitution in the delta chain (De Jong 1971a, b). Man and chimp both differ from _Gorilla_ by one alpha and beta chain substitution. Averaging the distance between the three available prosimians (sifaka, _Lemur_ and bush baby) and five anthropoid alpha sequences, 19 differences or substitutions are observed (Goodman _et al_., 1971). Assuming a prosimian-anthropoid divergence time of 70 million years, a rate of substitution of one amino acid per 7.3 million years is obtained. Cladistically man, chimp and gorilla are equally distant. Thus, the one alpha substitution in the gorilla lineage indicates a time of separation of the three forms on the order of 0 - 3.7 million years ago. The African apes and man have approximately 5-6 alpha chain substitutional differences from _M_. _mulatta_ and _M_. _fuscata_. With six differences a total of 42 million years of divergence or 21 million years per lineage would be expected which is in good agreement with the immunologically predicted date.

Previous estimates of the rate of evolution of hemoglobin are about one substitution per 3.5 million years (Dickerson, 1971). If man and chimp diverged 15 million years ago, then it would be expected that they would differ by approximately 8-9 amino acid substitutions. The average Old World monkey differs by some 14 nucleotide substitutions from the African apes and man in both alpha and beta chain. This difference equates to a time of divergence of some 24.5 million years for cercopithecoids and hominoids.

An analysis of the available myoglobin data yields similar results (Romero-Herrera et al., 1973). Man and chimp differ by one amino acid. The rate of substitution of myoglobin between the anthropoids and prosiminans assuming 70 million years time of divergence and given an average of 21 amino acid differences between the two taxa is 6.6 million years per substitution or 3.3 million years per two lineages. Since man and chimp differ by one substitution this gives a best estimate from 0 - 3.3 million years for their divergence. A time of separation of 15 million years for these forms would lead us to expect between 4 and 5 substitutions. Man and chimp differ from the Old World monkeys by an average 6.5 substitutions. This predicts a divergence time estimate of 21.5 million years given a rate of 1 substitution per 6.6 million years.

The sequence data are all concordant in showing that man and chimp are extremely closely related at the protein level. Out of the 430 amino acids sequences from alpha and beta hemoglobin myoglobin, and fibrinopeptides, man and chimp differ by only one substitution. The calculation of an absolute time of divergence of man and chimp based on such small sequence difference is of course statistically nonvalid. There is in all probability no difference between 0, 1 and 2 substitutions when 1 is expected. However the range of dates predicted by the small sequence differences is all in the direction of much less than 15 million years. In fact using the assumption of a divergence date of 15 million years and the rates of evolution of the molecule yields an expected number of substitutions far greater than what is actually found. In contrast where enough data is available for analysis the date of the cercopithecoid-hominoid divergence using the actual sequence difference given the calculated rate of evolution of the molecule is very close to what the immunological data would predict.

Three other immunological studies have some relevance. The first is the composite immunological studies of Goodman (Goodman et al., 1971, 1973). Goodman has converted his antigenic distance into a relative distance (Goodman and Lasker, 1973). As shown in Table 1-18 the ratio of the man-chimp distance relative to the catarrhine-platyrrhine index of 1.0 is 0.12 which agrees well with an albumin ratio of 0.12 and a transferrin ratio of 0.13. Since the direct ratios agree so well a time of divergence based upon this ratio would show close agreement. The second immunological study is that of Nonno et al. (1969) using carbonic anhydrase B and C isozymes. With antisera prepared to purified carbonic anhydrase B from Homo sapiens, chimp differed by 4 ID units, the Old World monkey average was 55 (5 species), and the New World monkey average of 3 species was 84. Values very similar to these are obtained with anti Homo sapiens transferrin. Again the data indicates the close genetic similarity of man and chimp.

A third immunological study is that of Hanke et al. (1973). Rabbit antisera were directed to the purified lysozyme from human and baboon. With the antisera prepared to the lysozyme of Homo sapiens the lysozyme of Pan shows no difference while Gorilla is 32 units distant. However, the lysozyme of Pongo is virtually indistinguishable from that of human. The six Old World monkey species tested differed by an average of 120 immunological distance units. The three New World monkeys differed by an average of 133 units. From a baboon perspective human and chimp differ by 66 units while gorilla is 38 units and orang is 76 units distant. The three New World forms are an average of 36 units distant from baboon. The results of reciprocal tests are not in close agreement as from anti human lysozyme, baboon is 127, and human is 66 with the reciprocal anti baboon lysozyme measurement.

The close genetic relationship of man and chimp is emphasized by the lack of differences between the lysozymes of these two forms as measured by microcomplement fixation. Yet, the gorilla lysozyme differs from that of human by 32 units which represents approximately 6% sequence difference (Hanke et al., 1973). This difference if it is real is the largest sequence difference detected between the proteins of man and the African apes. There is some question whether this difference may be an immunological artifact and not a real sequence difference. For example, from the baboon perspective the gorilla is 28 units less distant than either chimp or human. Thus, it is unclear whether there is an actual sequence difference of this magnitude or whether the difference is due to the imperfect correlation of immunological difference and sequence difference.

It has become possible to measure genetic difference by nucleic acid hybridization and data are now available on several primate species (Kohne, 1970; Kohne et al., 1972; Hoyer et al., 1972). Using "non repeated" DNA sequences, Kohne has estimated that human-chimpanzee hybrid DNA dissociates at a temperature of 1.5°C lower than the dissociation temperature of reannealed native human DNA (Kohne, 1970; Kohne et al., 1972).

On the other hand Hoyer (Hoyer et al., 1972) has estimated that the difference in dissociation is 0.7°C for human and chimp. The absolute values of ΔTm of man and chimp are certainly different. However, what is important is the relative differences. If a human-capucin difference of 10.5°C is taken as representative of a platyrrhine catarrhine distance and 35 million years is used as the time of separation of the two infraorders, a human chimp difference of 1.5°C translates to a 5 million years divergence time. Similarly a difference of 6.3°C between human and green monkey translates to a time of separation of 21 million years. The human-gibbon differences of 3.5°C translates to a divergence estimate of 11.7 million years. All are in excellent agreement with the time of divergence calculated using the immunological data.

The additional data provided by Hoyer (Hoyer et al., 1972) provides us with cladistic information, as a second reference point is provided. Radioactive orang DNA is used in the comparisons along with the radioactive human DNA. The data suggest that from an orang perspective the gibbon is as far removed as are the African apes and man. Secondly, gorilla, chimp and human seem to form a unit with somewhat more evolution occurring along the gorilla lineage. From a human perspective the human-chimp-gorilla distance is 0.18 of the human-green monkey distance (1.05°C vs. 5.7°C). This works out to a time estimate of 3.5 million years if 20 million years is used for the cercopithecoid-hominoid divergence. Similar analysis shows the Homo vs. Pongo vs. Hylobates divergence to have occurred 10 million years ago. From a radio active orang DNA perspective the human-chimp-gorilla vs. orang distance is 2.0°C compared to a green monkey-orang difference of 4.3°. This yields a divergence time estimate for human and orang of 9.3 million years again assuming a hominoid-cercopithecoid separation time of 20 million years.

Table 1-25 shows a summarized statement of what various macromolecules reveal of the genetic and temporal relationships of man and chimp. The most valid estimates for times of separation are those found for the hominoid-cercopithecoid and Homo-Hylobates divergences. These forms have had enough evolutionary time separating them so that their macromolecules have evolved sufficiently to give valid estimates of genetic distances. The text details how well these estimates from various macromolecules agree as to the times of divergence.

The man-chimp genetic distance is much smaller than either the Homo-Hylobates or the hominoid-cercopithecoid difference. With such small numbers seen in the sequences a valid statistical estimate of the time of separation is impossible. Enough sequence data are available to estimate an average rate of substitution for each molecule within the primates. Once this is determined it can be calculated what would be expected if a longer divergence time for human and chimp were in fact true. Upon analyzing the sequence and nucleic acid hybridization data for average evolutionary rates found within the primates, it is found that the data are consistent in indicating that the actual amount of time separating man and chimpanzee or gorilla is small. Enough of a

TABLE 1-25

Comparison of the Differences Found Between Man and Chimp in Their Macromolecules.

Dates of divergence are calculated on the basis of rates of evolution found for that specific molecule within the primates.

Source of Data	Observed Difference between Man and Chimp	Expected Difference Assuming 15 M.Y. Separation of Man and Chimp	Time of Divergence of Man and Chimp X 10^6 yrs.
Fibrinopeptide[a]	0	7	0 - 10.5
Haemoglobin[b]	0	8-9	0 - 3.7
Myoglobin[c]	1	4-5	0 - 3.3
DNA (Kohne)[d]	1.5° C	4.5° C	5.0
DNA (Hoyer)[e]	0.7° C	4.3° C	2.5

[a] Data from Wooding *et al*. (1972).

[b] Data from Goodman *et al*. (1971).

[c] Data from Romero-Herrera *et al*. (1973).

[d] Data from Kohne *et al*. (1972).

[e] Data from Hoyer *et al*. (1972). If an average of the distance from human to chimp and gorilla is used, then the divergence time estimate increases to 3.5 M.Y.

difference has accumulated between the hominoids and the cercopithecoids to indicate that the Homo-Hylobates distance is on the order of 10 million years.

Without access to other sources of information a range of from 0 to 10 million years with a mean of 4-5 million years is the best estimate that can be made of the time of separation of the African apes and man based upon their macromolecular differences. This is not to say that there is an equal probability of this divergence event occurring at any point within this range. Each additional source of macromolecular evidence, because of their close agreement in their estimation of the time of separation of man from the African apes, increases the height of the distribution curve that describes the probability vs. time plot. This additional data increases the probability that the actual time of divergence is in the range of 4-8 M.Y. The range narrows as the standard deviation of the distribution drops. The total macromolecular picture suggests then that the maximum probability for this divergence is from 4-8 M.Y. The probability rapidly slopes to zero on either side of this maximum probability estimate.

An additional source of data, that from fossils, may further narrow this range so that even stronger conclusions may be drawn in estimating times of separation of these taxa. Various hominid remains have been recovered from dateable East and South African plio-pleistocene deposits.

Leakey (Leakey, 1973) has ascribed over 100 fossil specimens from East Rudolph, Kenya to at least two different genera of hominids, Australopithecus and Homo. These fossils date from 3 to 1 million years. Similarly in the lower Omo basin of Ethiopia, Howell (Howell, 1969; Howell and Coppens, 1974) has recovered hominid remains from two main localities dating from 3 to 1.4 million years. Unquestioned hominid remains have also been discovered in South African deposits of unknown absolute dates; but these forms are certainly within the range of time of similar forms in East Africa (Howell, 1967; Brain, 1972). Earlier fossil specimens have been considered to be hominids, for example Ramapithecus (Simons, 1969, 1972; Pilbeam, 1966; Leakey, 1969). However, the status of Ramapithecus as a hominid has been questioned on morphological grounds (Andrews and Walker, 1973). The presence of a hominid in the fossil record before approximately 4 M.Y. remains to be demonstrated.

The range of time estimated for the divergence of man and the African apes based solely on differences in their macromolecules must be shortened in one direction as a result of paleontological evidence. The minimum time for this divergence using dates from deposits containing hominids cannot postdate 3-4 M.Y. On the opposite end, macromolecular comparisons restrict the maximum divergence time to approximately 10 M.Y. However, the weight of macromolecular evidence strongly suggests that the separation of the lineages leading to Homo and Pan is nearer the recent end of this restricted range. It becomes increasingly difficult to reconcile a divergence time of man and the African apes of much more than 5 M.Y. with the growing body of molecular information and the remaining scarcity of suitable candidates for hominid ancestry that predates this time.

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II. THE FOSSIL EVIDENCE FOR HUMAN EVOLUTION

SOUTH AFRICA

History of the Discoveries and Early Geomorphologic Investigations

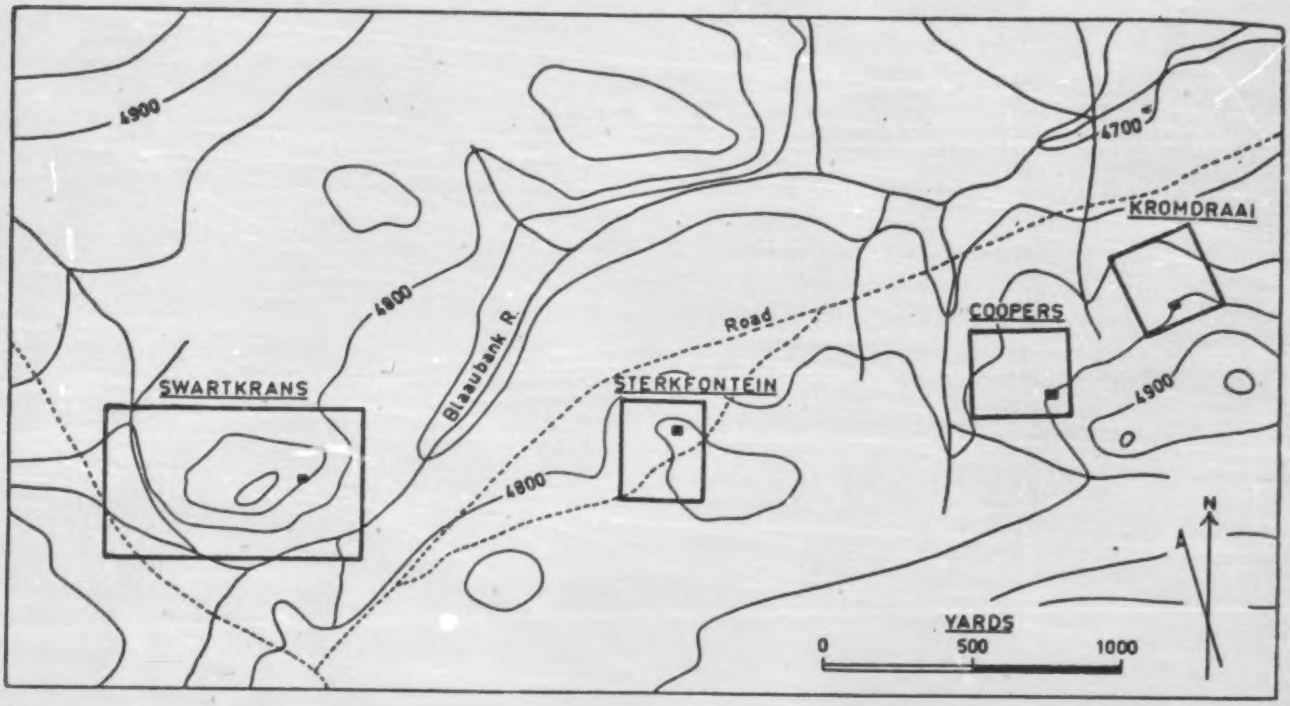
The sites of Sterkfontein, Swartkrans and Kromdraai are all grouped within the Blaaubank River Valley approximately six miles north of Krugersdorp, Transvaal, Union of South Africa. (Figure II-1.)

STERKFONTEIN. During 1936, Robert Broom was notified of a cave at Sterkfontein which had yielded a faunal assemblage similar to the one he had previously collected from another cave site. That year, Broom recovered from the deposits, with the help of the limeworks manager, the skulls of three baboons, a saber-tooth cat and an endocast of the brain of an australopithecine. Later search revealed numerous parts of the skull itself which was later named Plesianthropus transvaalensis. Several other hominid specimens were additionally recovered from the upper part of the deposit, but it wasn't until 1937 that specimens came to light from a horizon some 10 meters lower down. Commercial operations at the mine closed in 1939 and were not continued until 1946 when Broom renewed his investigations. On April 18th the most complete cranium was unearthed (STS 5) and was nicknamed "Mrs. Ples". The site was then visited by a geologist, Professor Lombaard, who reported that the cave fillings were of a uniform stratigraphical sequence and as a result Broon continued to extract specimens until January of 1949 when he began work at Swartkrans.

During 1956 Brain recovered numerous stone artifacts in breccia of the upperlevels of the west pit (= SE). The breccia of the west pit is continuous laterally with that of the upper type site but the two are probably separated by some temporal disconformity (Robinson and Mason, 1957).

During the field investigations of 1957, Mason and Brain excavated additional artifacts of the South African Middle Stone Age from refilled breccia

Figure II - 1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500
1000

From Brain, Trans. Mus. Mem. 11 (1958): 54.

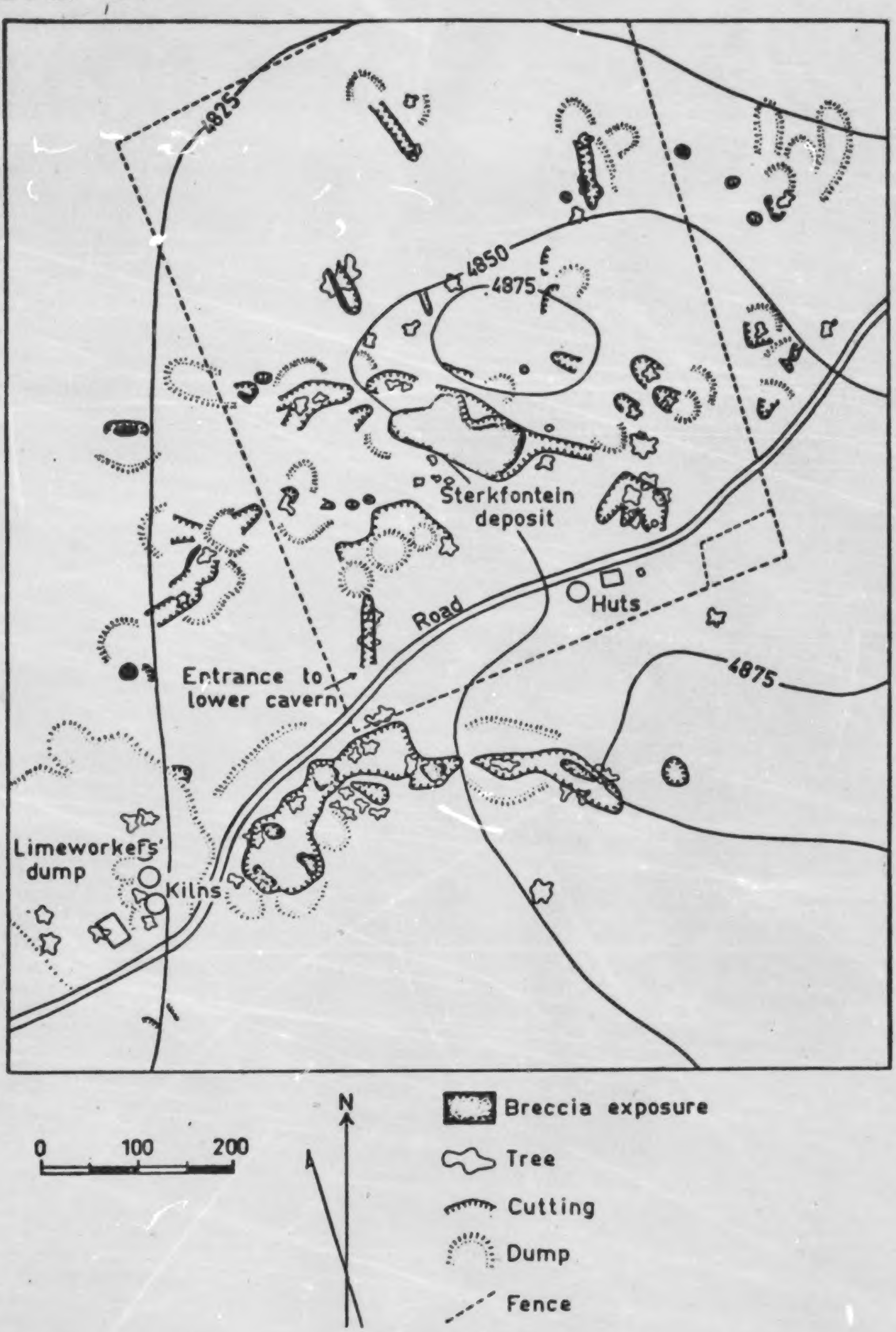
overlying older deposits. However, during the same year a volume of west pit breccia was excavated by Robinson, who was able to recover a series of artifacts and several teeth of what was described as Australopithecus, demonstrating the association between the hominid remains and the stone tools. These artifacts were classified by Mason as Late Olduwan. No stone tools have been found in association with Australopithecus at the type site (STS).

The Sterkfontein cave deposits at the type site have not been completely exposed. As a consequence, the extent of the deposition is not completely understood. Stratigraphical investigations were undertaken by Broom (1958) who showed that the plan of the cave was long and hall-like with a length of about 55 meters (Figure II-2,3). The roof is only partly eroded away and is preserved in area somewhat less than half the width of the cave. The original cave entrance was probably long and narrow and extremely precipitous, barring easy entrance to most animals. As a result, most of the hominid remains come only from the uppermost levels of the cave filling immediately underneath the dolomite cave roof.

Recent geomorphological investigations have demonstrated that the accumulation of the Sterkfontein cave was of considerably longer duration than previously believed. This work demonstrated the existence of an earlier bone-breccia under the thick travertine once regarded as the floor of the main deposit which extends downwards for a considerable depth (Tobias and Hughes, 1969).

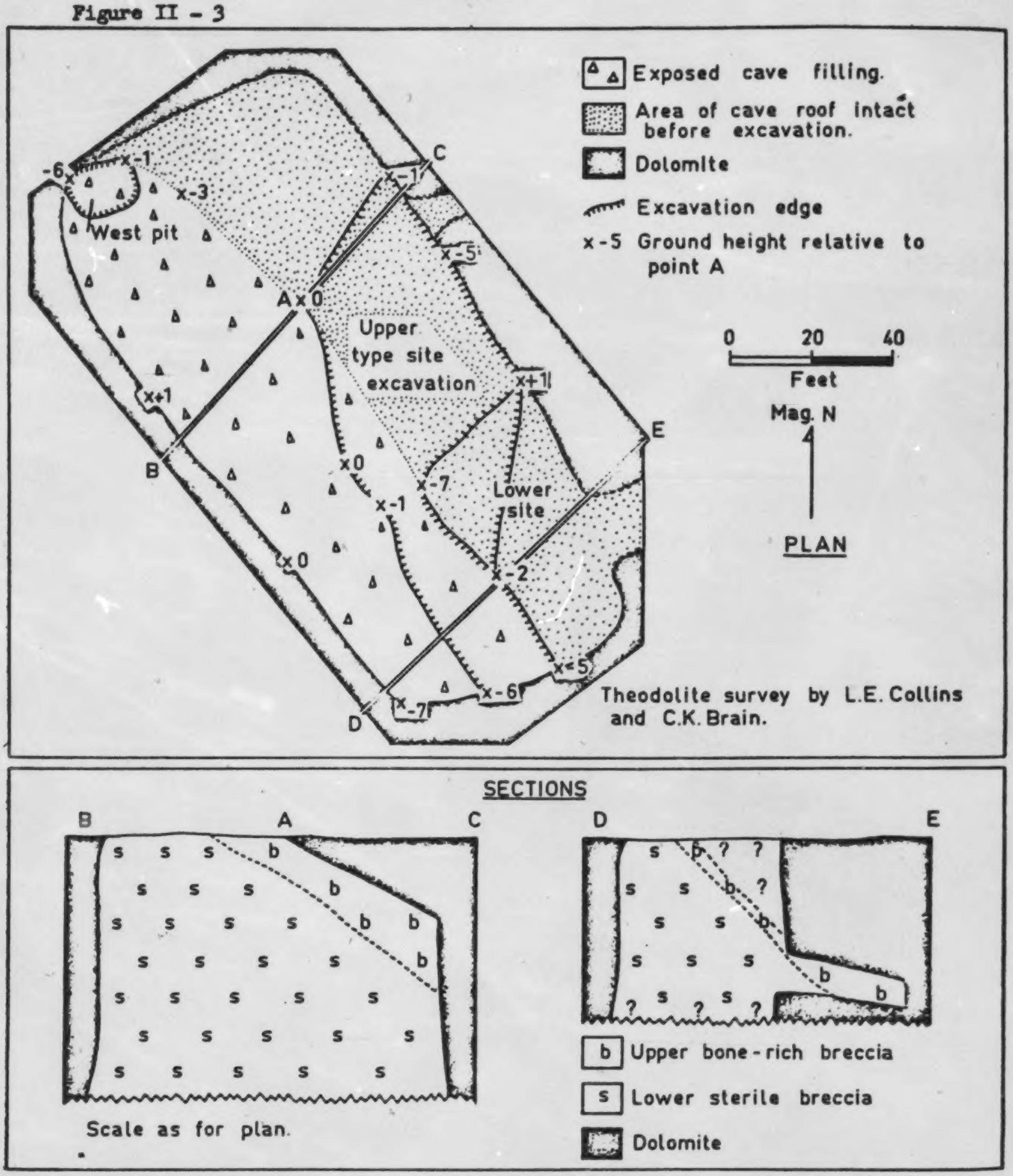
SWARTKRANS. Towards the end of 1949 excavations began at a nearby locality at Swartkrans. The first specimen to be recovered was a molar tooth of a new hominid species named Paranthropus crassidens and later numerous other fragments. During April 1949 a mandible fragment of another new hominid species was described as Telanthropus capensis. Excavations continued through 1949 but

Figure II - 2


4825
4850
4875
Sterkfontein deposit
Huts
Road
Entrance to lower cavern
4875
Limeworkers' dump
Kilns
0
100
200
N
Breccia exposure
Tree
Cutting
Dump
Fence

SITE PLAN OF STERKFONTEIN DEPOSIT.
From Brain, Trans. Mus. Mem. 11 (1958): 61.

Figure II - 3


Exposed cave filling.
Area of cave roof intact before excavation.
Dolomite
Excavation edge
x-5 Ground height relative to point A
0 20 40
Feet
Mag. N
PLAN
West pit
Upper type site excavation
Lower site
A x0
B
C
D
E
-6
x-1
x-3
x-1
x-5
x+1
x+1
x0
x-7
x-1
x0
x-2
x-5
x-6
x-7
Theodolite survey by L.E. Collins and C.K. Brain.
SECTIONS
B
A
C
D
E
s
b
?
Upper bone-rich breccia
Lower sterile breccia
Dolomite
Scale as for plan.

STERKFONTEIN SITE PLAN AND VERTICAL SECTIONS.
Brain, Trans. Mus. Mem. 11 (1958): 62.

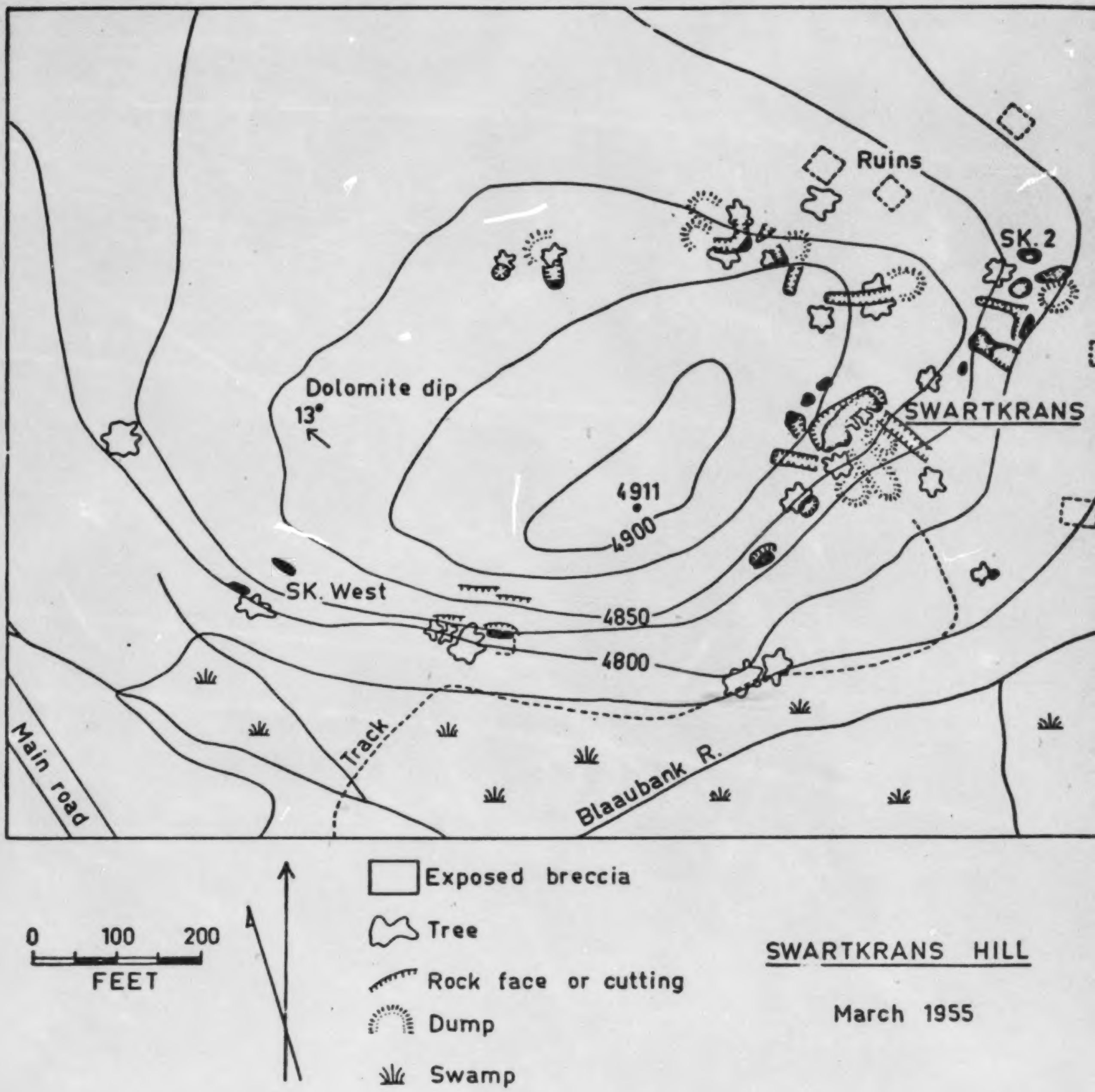
were halted by the commercial quarrying operations at the site until 1952.

The initial geomorphological investigations were done by Brain, who divided the Swartkrans cavern system into three parts: an inner, an outer, and a lower cave; the lower cave is connected to the surface by two nearly vertical shaft openings at its eastern end. The lower cave extends underneath the western part of the outer cave, separated from it by a dolomitic floor. The outer cave is separated from the inner cave by a raised floor section and the dolomite roof has been largely removed by erosion exposing the fossiliferous lower breccias. The outer cave was filled almost completely by an older, highly calcified pink breccia overlain in certain parts by a less heavily calcified brown breccia which nearly completely fills the inner cave. Most of the australopithecine remains have come from the pink breccia.

Brain (1958) developed the sequence of deposition at Swartkrans beginning with a travertine basal layer followed by a residual grey breccia. Overlying the residual deposit is the Phase I Basal Pink breccia separated from the lower deposits by an abrupt transition marking the point where the cave was first opened to the surface. At the top of the Phase I deposits the Basal Pink breccias are gradually replaced by Phase II breccias consisting of the previously listed outer cave pink breccia and the inner cave stratified brown breccia which is disconformably separated from the pink breccia. (Figure II - 4.)

KROMDRAAI. Excavations of this cave site began in 1938 when Robert Broom obtained the first hominid fragment which consisted of a palate and an in situ molar tooth. This specimen was obtained from the manager of the limeworks at Sterkfontein who himself had received the specimen from a local schoolboy. Further investigations led Broom to a nearby hill about a mile away from Sterkfontein. Additional specimens were recovered which belonged to a nearly

Figure II - 4


Ruins
SK. 2
Dolomite dip
13°
SWARTKRANS
4911
4900
SK. West
4850
4800
Main road
Track
Blaaubank R.
0
100
200
FEET
Exposed breccia
Tree
Rock face or cutting
Dump
Swamp
SWARTKRANS HILL
March 1955

MAP OF SWARTKRANS DEPOSIT.
Brain, Trans. Mus. Mem. 11 (1958): 75.

complete cranium lacking only some of the upper teeth. Broom designated the reconstructed skull (TM 1517) as the type specimen of a new genus and species Paranthropus robustus.

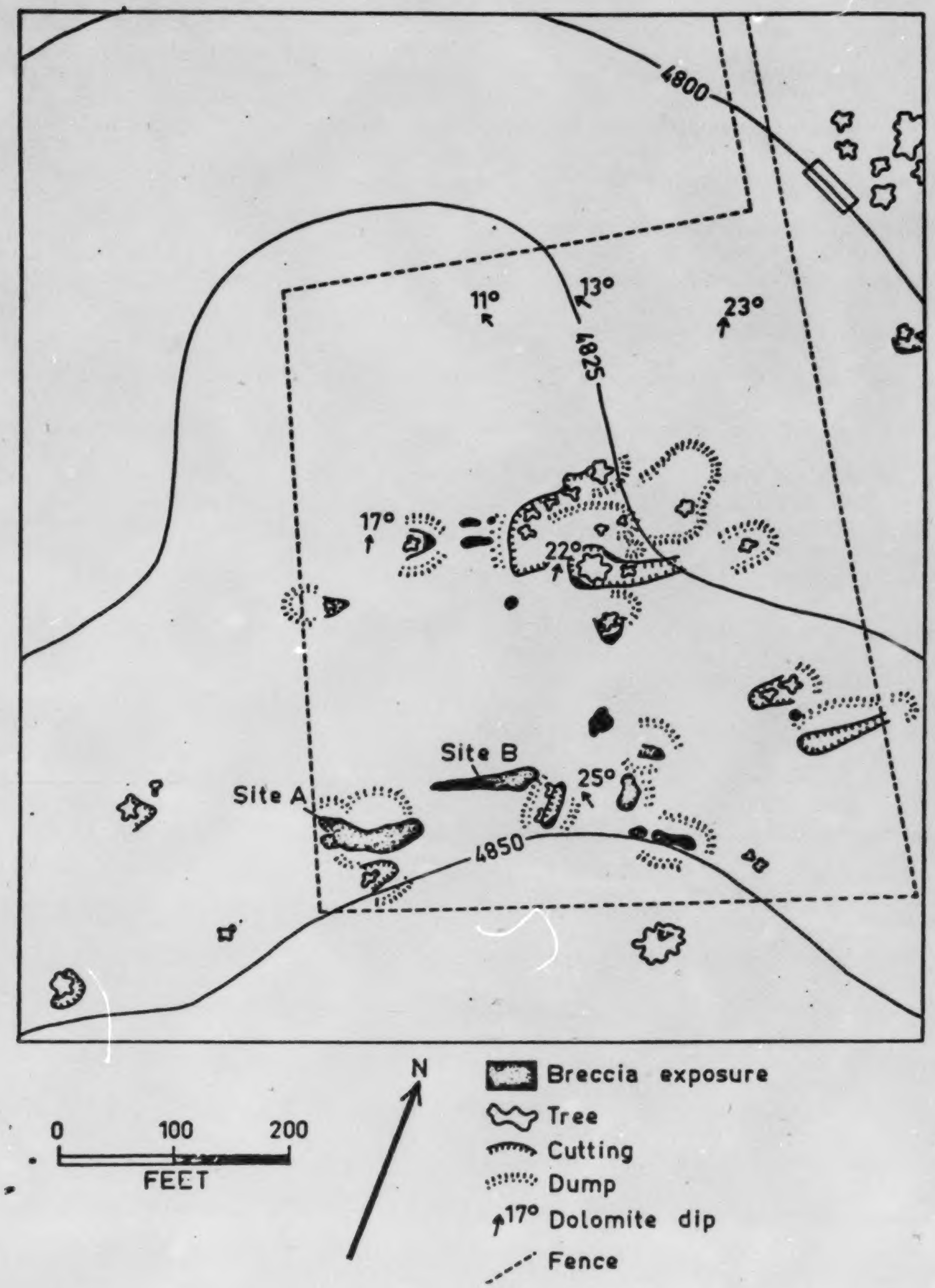
Further investigations at Kromdraai were delayed until 1941. Excavations at that time exposed a mandible with nearly complete milk dentition of an adolescent. Work was again halted until March 1955 when discoveries by C. K. Brain increased the number of hominid fossils by unearthing additional isolated teeth and large numbers of fragmentary bone.

The two sites, Kromdraai A and B, are both elongated but relatively narrow. At Site A the dolomite roof has been totally eroded off and only part of the roof remains at Site B excavated by Brain. The cave was completely filled with breccia to the roof embedding the stalactites which once hung down. The breccia in the cave could be divided into two types: the coarse-grained stony breccia which was deposited at the eastern end of the site and the remaining finer-grained stratified material. The original cave entrance was no doubt directly above the eastern end of the cave for the surface-derived material which washed into the cave was naturally sorted with the heavier stony fraction remaining below the entrance and the finer material carried further into the cavern. (Fig. II-5.)

MAKAPANSGAT. The limeworks cave is situated on the Makapansgat Farm about ten miles to the northeast of Potgietersrust in the Central Transvaal. The earliest reference to the site was made by Dart (1925) when he described a very fragmented and largely unidentifiable bone assemblage sent to him by W. Eitzman, a visitor to the site. Much of the assemblage had been blackened as if burnt and Dart's conclusions were that man had been responsible for the bone accumulation.

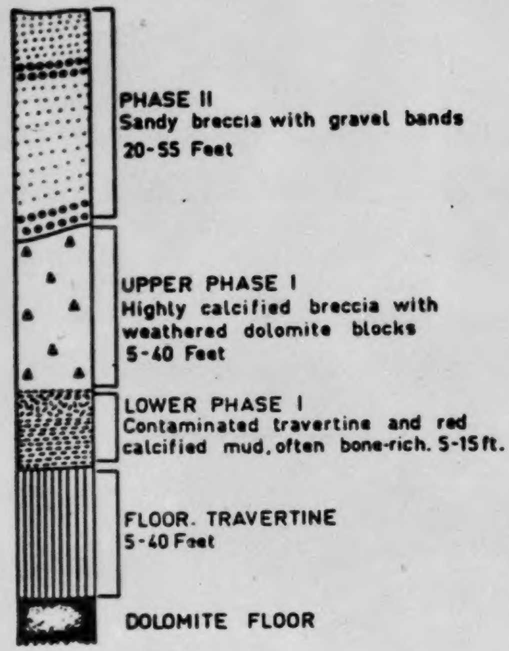
In 1947 the first human remains were discovered and consisted of a fragmented occipital. Later, in 1948, an adolescent male mandible, cranial fragments, teeth and an adolescent pelvis within the extensive associated faunal

Figure II - 5


4800
4825
4850
11°
13°
23°
17°
22°
25°
Site A
Site B
N
0
100
200
FEET
Breccia exposure
Tree
Cutting
Dump
17° Dolomite dip
Fence

MAP OF KROMDRAAI DEPOSIT.
Brain, Trans. Mus. Mem. 11 (1958): 91.

Figure II - 6


PHASE II
Sandy breccia with gravel bands
20-55 Feet
UPPER PHASE I
Highly calcified breccia with weathered dolomite blocks
5-40 Feet
LOWER PHASE I
Contaminated travertine and red calcified mud, often bone-rich. 5-15 ft.
FLOOR. TRAVERTINE
5-40 Feet
DOLOMITE FLOOR

Simplified stratigraphy
of the Makapansgat Limeworks
Deposit. (From Brain (1958): 107)

remains were also recovered from the Limework's dump. Because Dart believed that the hominid remains were of those individuals who had been responsible for the burnt bones, a new species of hominid, Australopithecus prometheus, was created.

During the middle 1950's additional hominid remains were recovered along with a collection of several stones showing artificial fracture. It was the opinion of Brain, van Riet Lowe and Dart that the horizon which had yielded the tool culture (= Kafuan) was contemporaneous with that which had yielded the hominid remains.

An additional discovery of an australopithecine maxilla in 1955 overlying the pebble-tool stratum indicated a clear association between the tools and the hominids.

The majority of the Makapans cave roof, as at Kromdraai, has been removed by erosion exposing the consolidated breccia to the surface over a considerable area. The original cave has been described as a subsidence rather than a solutional geomorphologic feature. This interpretation required that a large solution cavern existed below the present cave and the roof of this solution cave collapsed creating a new cave above. The original subsidence must have occurred at some depth below the surface which created no immediate connection with the land surface. Thus the explanation for the relatively uncontaminated travertine deposit which was deposited over the basal dolomite floor. According to Brain (1958), once the opening developed it remained small for a considerable period of time which would account for the Phase I deposits of contaminated travertines and calcified muds. (The Lower Phase I deposits have yielded the most hominid material.) A sudden enlargement of the opening initiated the apparently rapid accumulation of the Phase II deposits which, except for the southwest rear corner of the cave (= "central collapsed area"), eroded away. A simplified profile of the Makapansgat LD deposit is shown in Figure II - 6. Continual unstability of the basal dolomite floor is evidenced by the presence of large cracks which lend further evidence supporting the hypothesis of the existence of a lower cavern. (Figure II - 7.)

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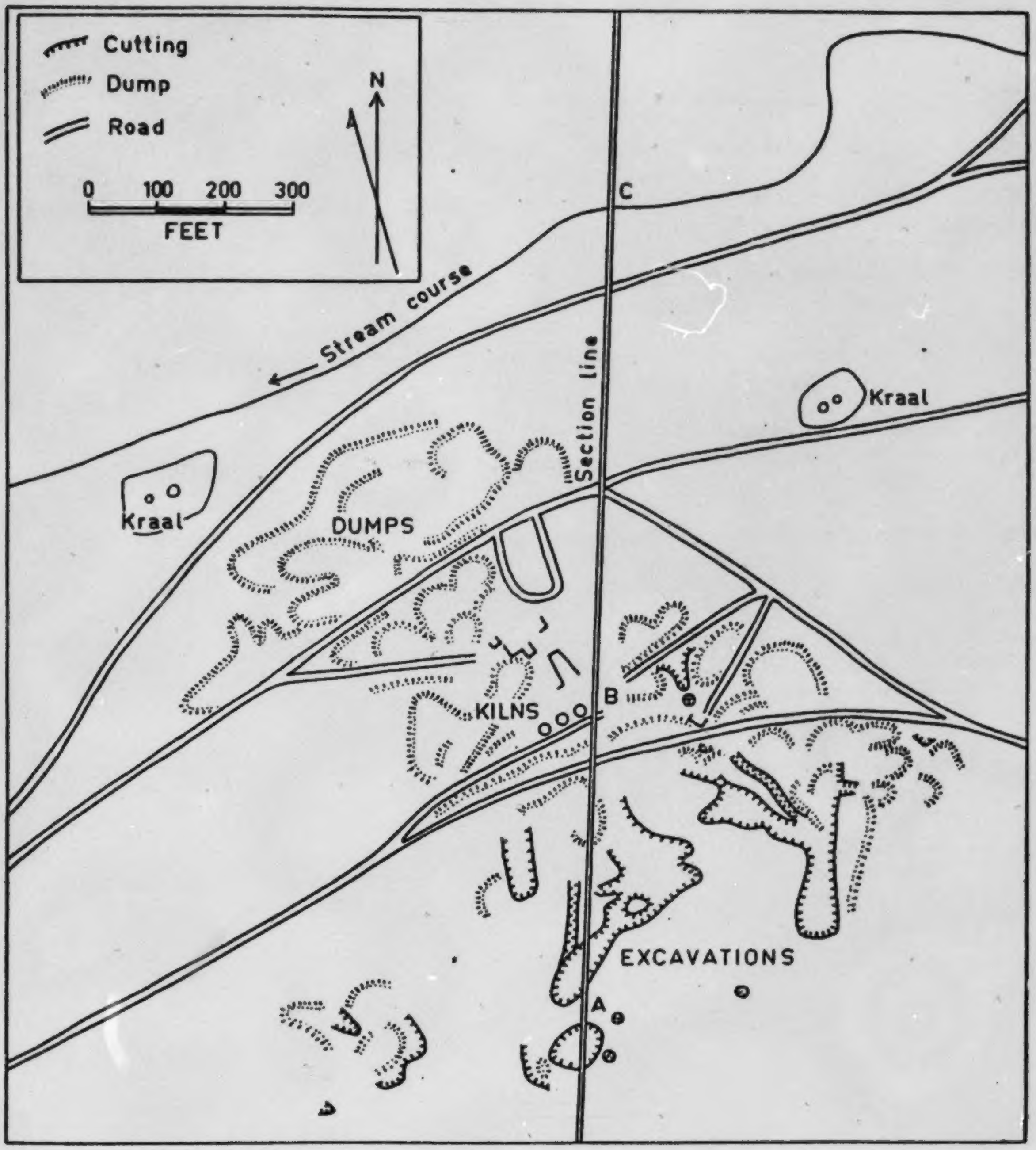
[1] The Swartkrans cave was abandoned until C. Brain began new investigations in April 1965. Excavations of undisturbed breccia were begun and a representative sample fauna of over 14,000 bone fragments was recovered. These investigations further showed the existence of a still older breccia occupying the eastern extension of the site and separated from the normal australopithecine-bearing deposit by an unconformity.

Figure II - 7


Cutting
Dump
Road
N
0
100
200
300
FEET
C
Stream course
Section line
Kraal
Kraal
DUMPS
KILNS
B
EXCAVATIONS
A

MAP OF MAKAPANSGAT LIMEWORKS DEPOSIT.
From Brain, Trans. Mus. Mem. (1958): 104.

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> ABSTRACT: Further evidence of the presence of a second hominid species at Swartkrans locality was obtained in 1969 when the SK-847 specimen was discovered by us to represent the same individual as the SK-80 maxilla. The SK-847 specimen had previously been regarded as robust australopithecine, whereas the latter was first attributed to *Telanthropus capensis* and subsequently to a species of the genus *Homo*. Recent criticism of our interpretation of these remains has not evaluated and analyzed critically the primary fossil evidence. Instead it relies on a strict adherence to an as yet unsubstantiated hypothesis that posits only a single hominid species at any point in space and time in the Cenozoic history of Hominidae.

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CORRELATION AND AGE OF THE SOUTH AFRICAN HOMINID SITES

Earliest attempts at assessing the age of the hominid sites in South Africa were based on analysis of the fossil faunal remains. Ewer (1955, 1956) believed that the relative ages of the sites followed the sequence of Sterkfontein and Makapan, both of a similar age, preceding Swartkrans and finally Kromdraai. Taung was believed to be the oldest site, though this view had been criticized by Wells (1969).

To the faunal sequence dating, climatic evidence was added by Brain (1958) giving the results of sand grain angularity (porosity) determinations and the chert-quartz ratios yielding approximately the same results as the faunal analysis. Brain concluded from his studies that a number of climatic changes had occurred in South Africa during the Pleistocene period. He based his conclusions on the following analyses: (a) angularity of quartz and grains. Such grains found in dolomite soils tend to be more rounded in shape with average rainfall between 400-750 mm, more angular with rainfall in excess of 900 mm and intermediate in areas with less than 350 mm rainfall. According to Brain, quartz components within the dolomitic rock is angular and a wetter climate dissolves out greater quantities of quartz. In drier settings, weathering of the dolomite is slower so that the released grains are altered and smoothed with time. In the very dry climates, the rounding process is affected by calcite cement adhering to the quartz grains. This analysis of angularity of quartz grains has several problems, however, the most difficult being that more than one environmental factor (i.e., rainfall) is responsible for reduction of the angularity of the material. Weathering of quartz involves at least five factors, none of which have had controls established. Certainly rainfall is one such factor, time of exposure, distance of transport, slope of transport, and the Ph of the rainfall are others which must be accounted for. Changes in any of these variables will have some effect on the weathering process, the exact effect has yet to be worked out experimentally.

(b) Ratio of chert to quartz. Determinations of the ratio of chert and quartz grains in local bedrock and local soil were made. Excess of quartz grains in the sedimentary column was attributed to additional earlier contributions to the admixed soils.

(c) Sediment color. Hillside dolomite soils exposed to humid conditions tend to be brownish, soils exposed to more arid conditions are more reddish.

From these data it was suggested that rainfall in South Africa varied considerably during the lower Pleistocene, and that the deposits at Makapansgat and Sterkfontein were accumulated during dry conditions; those at Swartkrans and Kromdraai were accumulated during later wetter (pluvial) conditions. These arguments were contested by Butzer (1971), who claimed that the finer cave compositions were made under identical geomorphologic conditions. The residual soil products of many ages making up the cave deposits were all swept together into the cave opening in the same colluvial wash. Erosion would have occurred because of an ineffective vegetation mat indicating an overall drier climate. Butzer concludes that the same reasoning applies to the red, sandy cave-fill at Taung. This does not mean that the rates and modes of soil formation outside the caves did not vary through time, but the suggestion was that variations in soil formation outside the caves were not contemporary with the periods of active erosion and consequent cave filling.

The cumulative thickness of the cave deposits suggested to Butzer that the Transvaal cave fills occurred over a minimum of several tens of thousands of years and possibly several hundreds of thousands of years, which raises the question of contemporaneity of similar cave stratigraphy at two or more sites.

In a recent review by Partridge (1973) the analysis of cave openings and fillings were put within a sequence of local erosional cycles and nick-point recessions which resulted in valley widening in the three drainage basins in which cave sites are located: (1) the Limpopo-Magalakwin-Makapan drainage system containing the Makapansgat Limeworks site, (2) the Limpopo-Crocodile-Bloubank drainage system containing the Sterkfontein and Swartkrans sites, and (3) the Orange-Vaal-Harto-Buxton drainage system containing the Taung site at the Buxton lime quarry.

Erosion within these drainage systems resulted in the retreat of the land surface and consequent exposure of cavern interiors to the outside through vertically enlarged joints (aven). Once opened the cavern was filled with externally derived hillside soil as well as with hominids and other animals. To date the earliest accumulation of the cave deposits, the time period which elapsed between the arrival of the new erosion cycle opposite the site and recession of the valley side to the point of exposure of the cavern to the outside was determined. From such an analysis a date of 3.7 million years was given for Makapansgat limeworks, 3.3 million years for Sterkforntein, 2.6 million years for Swartkrans and less than .9 million years for Taungs, the deposit of which accumulated on the valley flank at Buxton subsequent to the last erosion cycle. This work was criticized by Butzer (1974: 416).

Recent faunal analysis has suggested that the Taung site is much younger than previously believed. Reviews of the primate fossils at Taung reveal that two species of Papio are found in common with those from Swartkrans and Kromdraai and the most common cercopithecoid Parapapio broomi from Sterkfontein and Makapansgat is absent from the deposits at Taung.

With a comparision of fossil suids from Sterkfontein and Makapansgat and that of Elephes recki from Makapansgat with those of the well-calibrated lineages from East Africa, Cooke (1970) suggested that the South African sites may be on the order of 2.5-3.0 million years old. Maglio (1973) agreed that these

South African sites seemed to correlate best with the East African faunal succession equivalent to middle Shungura at Omo. Cooke has further suggested that Swartkrans is at least as old as Bed I, Olduvai (approximately 1.8 million years, Upper Member).

Tobias (1973) reports that at two South African sites, Makapansgat and Sterkfontein, recent excavations have revealed considerably greater depth of the breccia deposits. During the 1973 field investigations, Tobias located considerably older lower breccia below the "basal" travertine floor which proved to be bone-bearing. The deposits of those bone breccias yielding fossil faunal forms comparable with the East African faunas are considerably above the travertine floor.

That the evidence suggests a much older date for the cave opening than for calibrated fauna is understandable in the light of the estimated periods of time it took for the caves to be filled.

The most recent faunal analysis of the fossil remains at Sterkfontein has been completed for the Bovidae. The analysis of the fossil bovids provides interesting information concerning possible time differences between the two main hominid site units, STS and SE. Tobias has long believed that the hominid remains uncovered at the extension site (SE) were more advanced than the Australopithecus remains found at the type locality (STS) and the faunal comparison indicates that at least three distinct chrono-assemblages are present. As described by Vrba (1974), Phase A is associated with the STS australopithecine assemblage and is similar to that found at Makapansgat (= Sterkfontein Faunal Span). Phase B is associated with the extension site (SE) hominids and resembles both Kromdraai A and Swartkrans though possibly closer to the latter in terms of species present (= Swartkrans or Cornelia Faunal Span). The similarity of tools from the SE site and from Swartkrans to the developed Olduwan assemblages has been reported by Mary Leakey (1970).

Phase C is of Middle Stone Age (= Florisbad or Florisbad-Vlakkraal Faunal Span) and only two bovid species of this assemblage are extinct forms.

The evolution of bovids at Sterkfontein indicate a change in environmental conditions possibly because of a decrease in rainfall between Phases A and B (contra Brain, 1958) which throws the problem of environmental reconstruction into further confusion.

The first published suggestion that some major South African fossil assemblages could be arranged in some chronological sequence (= Faunal Spans) was made by Wells (1962). Recent work by Vrba (1975) has suggested that the Swartkrans assemblage encompasses more than one component, one of which is at least considerably later than the assemblage associated with the Australopithecines. The present data also suggest that localities at Kromdraai, the faunal site (KA) and the australppithecine site (KB) as well as the Sterkfontein extension site (SE) should not be included in the Swartkrans Faunal Span but perhaps in the succeeding Cornelia Faunal Span.

The patterns of accumulation of bone materials at the different sites have resulted in interesting speculations. According to Vrba (1975), Brain (1970) and Ewer (1967), the accumulation at the STS site is more likely to be the result of the action of large carnivores, possibly sabre-toothed cats. This would account for the high average weight determined for the bovid species represented in the assemblage. Brain (1970) has produced an interesting analysis that the predominant contribution to the SKA and KA assemblages may have come from leopards. The restricted medium weight range of the prey suggests smaller sized predators. In this light the hominids from these localities are more likely to have been prey rather than predators.

The KB and SKB assemblages are different in that the bone remains are extremely fragmented and represent a high percentage of juvenile individuals, suggestive of a predator who specialized in small prey. With the evidence of the existence of stone tools at these sites (including locality D-16 at Sterkfontein with a Middle Stone Age industry), the suggestion was made (Vrba 1975: 303) that the predator in this case was a hunting hominid.

Finally at the Sterkfontain Extension Site (SE) the existence of numerous stone tools suggests that this locality may also have been a hominid occupation site. The accumulation pattern is different, however, from Skb and KB in that the assemblage is represented by species of all weight classes and that juveniles represent a markedly lower percentage in the remains. This data is consistent with the hypothesis that the SE remains are the result of hominid scavenger activity.

The pattern, therefore, of the bovid assemblages gives further evidence for establishing a relative sequence of events for some of the South African deposits: STS, Ska, KA, SE, KB, Skb and D-16 (older to younger).

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Includes plan of Sterkfontein excavation site (after Tobias and Hughes), distribution of bovid species between STS and SE, and suggested distribution of bovid species throughout all site units at Sterkfontein.

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Bovid fossil remains suggest a tentative chronology for the seven cave assemblages, from Sterkfontein, Swartkrans, and Kromdraai, from which they are derived. They also suggest that, during the almost 2 million years of South African hominid and faunal Pleistocene history encompassed by this succession of assemblages, certain changes in vegetation cover and cave accumulation patterns may have occurred in the Sterkfontein Valley.

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CATALOGUE OF FOSSIL HOMINIDS
SWARTKRANS

SK 1	Left M_2	1949	Trans. Mus. Mem. 9: 107
SK 2	Right I^1	1948	Trans. Mus. Mem. 9: 23
SK 3	Right I^2	1948	Trans. Mus. Mem. 9: 26
SK 4	Right $\underline{C}$	1948	Trans. Mus. Mem. 9: 41
SK 5	Left M_2	1949	unpublished
SK 6	Adolescent mandible, left P3→M3, right P4→M3, holotype *Paranthropus crassidens* Broom 1949	1948	Trans. Mus. Mem. 6
SK 7	Right P_4	1949	Trans. Mus. Mem. 9: 73
SK 8			
SK 9	Left P_4	1949	Trans. Mus. Mem. 9: 73
SK 10	Left corpus of mandible, M2-M3	1949	
SK 11	Maxillae with left P3-M3, right P3-M2	1949	Trans. Mus. Mem. 9: 60, 86, 91
SK 12	Mandible with left/right P4-M3, palate, maxilla	1949	Trans. Mus. Mem. 9: 60, 73, 112
SK 13/14	Maxillae, left P3-M3, right P3-M3	1949	Trans. Mus. Mem. 9: 55, 60, 81, 86, 90
SK 15	Mandible, left M1-3, right M2, M3 holotype *Telanthropus capensis*	1949	AJPA 11: 462
SK 16	Left M^3	1949	Trans. Mus. Mem. 9: 91
SK 17	Right M^1	1949	Trans. Mus. Mem. 9: 81
SK 18	Lower left P3, associated proximal end of radius	1949	AJPA 11: 462
SK 19	Right $\bar{M}$	1949	unpublished
SK 20	Left M_1	1949	unpublished
SK 21	Maxilla fragmented left C-M3	1949	unpublished
SK 22	Right M^3	1949	Trans. Mus. Mem. 9: 112
SK 23	Female mandible with teeth	1950	Trans. Mus. Mem. 9: 35, 36, 46, 69, 73, 101, 107, 112

SK 24	Left P^3	1949	Trans. Mus. Mem. 9: 55
SK 25	Mandible with left P4-M2, right P4-M2	1949	Trans. Mus. Mem. 6: 22
SK 26			
SK 27	Juvenile male (?) cranium, facial bones damaged, left I2, dm2, M1, right M1, unerupted C	1949	Trans. Mus. Mem. 6: 26-28
SK 28	Left P^3	1949	Trans. Mus. Mem. 9: 60
SK 29	Right $\bar{C}$	1949	Trans. Mus. Mem. 9: 46-48
SK 30	Left P_3	1949	Trans. Mus. Mem. 9: 69
SK 31	Right M^3	1949	Trans. Mus. Mem. 9: 91
SK 32			
SK 33			
SK 34	Mandible in two halves, left P4-M3, right I1-M3	1949	Trans. Mus. Mem. 6: 16-18
SK 35	Left M^1	1949	unpublished
SK 36	Right M^3	1949	Trans. Mus. Mem. 9: 91
SK 37	Mandible, left M2, M1	1949	Trans. Mus. Mem. 9: 107
SK 38	Right $\underline{C}$	1949	Trans. Mus. Mem. 9: 41
SK 39	Right P^4	1949	unpublished
SK 40	Left I^1	1949	Trans. Mus. Mem. 9: 23
SK 41	Right M^3	1949	Trans. Mus. Mem. 9: 91
SK 42	M^2	1949	unpublished
SK 43	Right P_4	1949	AJPA 11: 462
SK 44	P^3	1949	unpublished
SK 45	Right corpus mandible, M1-2	1949	Trans. Mus. Mem. 6: 111-112
SK 50	Male(?) right innominate, associated distal humerus	1949	Trans. Mus. Mem. 6: 90-94
SK 55/55b	Juvenile maxilla, left I^1-P3, M1, dm2, M2	1949	Trans. Mus. Mem. 9: 23, 26, 41, 55, 81, 69, 101, 112, 140

SK 57	Fragmented palate, left P3-M3, right P3-M1	1949	Trans. Mus. Mem. 9: 55, 60
SK 60			
SK 61	Juvenile mandible, right and left dI^1-dm2, erupting M1	1949	Trans. Mus. Mem. 9: 101, 130, 131, 134, 140
SK 62	Juvenile mandible, left dI2-dm2, M1 unerupted, right I^1-dm2	1949	Trans. Mus. Mem. 9: 35, 130, 131, 134, 140
SK 63	Juvenile mandible, left/right dc-dm2, m1	1949	Trans. Mus. Mem. 9: 35, 37, 46, 101, 131, 134, 140
SK 64	Juvenile mandible, right dm1, dm2	1949	Trans. Mus. Mem. 9: 134, 140
SK 65	Maxilla, left I^1-P4, right C	1949	Trans. Mus. Mem. 9: 23, 26, 41, 55, 60
SK 66	Juvenile maxilla, roots dc, dm1, dm2	1949	Trans. Mus. Mem. 9: 26
SK 67	Right I^1 possibly belonging to SK 65	1949	unpublished
SK 68	Left I^1	1949	Trans. Mus. Mem. 9: 23
SK 69	Left I^1	1949	Trans. Mus. Mem. 9: 23
SK 70	Left I^2	1949	Trans. Mus. Mem. 9: 26
SK 71	Right I^2	1949	Trans. Mus. Mem. 9: 26
SK 72	Left P_3	1949	Trans. Mus. Mem. 9: 69
SK 73	Right I^1	1949	Trans. Mus. Mem. 9: 23
SK 74a	Mandible with left P3-M2, right I2-M2	1949	AJPA 8: 299-300
SK 74b	Right I_1	1949	Trans. Mus. Mem. 9: 35
SK 74c	Right P^3	1949	unpublished
SK 75	Right M_3	1949	unpublished
SK 80	Fragmented maxilla, left I2-P3, same as SK 45	1949	Trans. Mus. Mem. 6: 111-112
SK 81	Left P_4, M_3	1949	Trans. Mus. Mem. 9: 73, 112
SK 82	Proximal right femur	1949	Trans. Mus. Mem. 6: 90-94

SK 83			
SK 84	First metacarpal	1949	Fossil Mammals of Africa 17
SK 85	Right $\underline{C}$/ fourth metacarpal	1949	tooth unpublished/Fossil Mammals of Africa 17
SK 86			
SK 87	Right $\overline{C}$	1949	Trans. Mus. Mem. 9: 46
SK 88	Left P_4	1949	Trans. Mus. Mem. 9: 73
SK 89	Left M^1	1949	Trans. Mus. Mem. 9: 81
SK 90	dm2, same as SK 89	1949	Trans. Mus. Mem. 9: 123
SK 91	dm1, same as SK 89	1949	Trans. Mus. Mem. 9: 128
SK 92	Right $\underline{C}$	1949	Trans. Mus. Mem. 9: 41
SK 93	Left $\underline{C}$, same as SK 85	1949	Trans. Mus. Mem. 9: 41
SK 94	Right $\overline{C}$	1949	Trans. Mus. Mem. 9: 46, 48
SK 95	Left $\underline{C}$	1949	Trans. Mus. Mem. 9: 41, 51
SK 96	Mandible, left X, P3	1949	Trans. Mus. Mem. 9: 46, 69
SK 97	Proximal right femur	1949	Trans. Mus. Mem. 6: 90-94
SK 98	Left M^2	1949	Trans. Mus. Mem. 9: 86
SK 99	Left P^4	1949	Trans. Mus. Mem. 9: 60
SK 100	Right P_3	1949	Trans. Mus. Mem. 9: 69
SK 101	Left P^3	1949	unpublished
SK 102	Left M^1	1949	Trans. Mus. Mem. 9: 102
SK 103			
SK 104	Right M_1	1949	Trans. Mus. Mem. 9: 101
SK 105	Left M^3	1949	unpublished
SK 106			
SK 107			

SK 108			
SK 109			
SK 820	$\bar{C}$	1952	Trans. Mus. Mem. 9: 46
SK 821	Portion of face with left P^3	1952	Trans. Mus. Mem. 9: 55
SK 822	Left P^3	1952	Trans. Mus. Mem. 9: 55
SK 823	Right P^3	1952	Trans. Mus. Mem. 9: 55
SK 824	Left P^4	1952	Trans. Mus. Mem. 9: 60
SK 825	Left P^4	1952	Trans. Mus. Mem. 9: 60
SK 826			
SK 826a	Maxilla fragment P3-M2	1952	Trans. Mus. Mem. 9: 86
SK 826b	Left P_4	1952	Trans. Mus. Mem. 9: 73
SK 827	Left P_4	1952	unpublished
SK 828	Left M_1	1952	Trans. Mus. Mem. 9: 101
SK 829	Left M^1	1952	Trans. Mus. Mem. 9: 81
SK 830	Left P_4	1952	Trans. Mus. Mem. 9: 73
SK 831	Right P_3	1952	Trans. Mus. Mem. 9: 69
SK 831a	Maxilla fragment, left M2-3	1952	Trans. Mus. Mem. 9: 86, 91
SK 832	Left M^1	1952	Trans. Mus. Mem. 9: 81
SK 833	Left M^1	1952	unpublished
SK 834	Left M^2	1952	Trans. Mus. Mem. 9: 86
SK 835	Left M^3	1952	Trans. Mus. Mem. 9: 91
SK 836	Left M^3	1952	Trans. Mus. Mem. 9: 91
SK 837	Right M^2	1952	Trans. Mus. Mem. 9: 86
SK 838			
SK 838a	Juvenile maxilla fragment, right dm2, m1,	1952	Trans. Mus. Mem. 9: 81, 128
SK 838b	left M_1	1952	Trans. Mus. Mem. 9: 101
SK 839	Juvenile maxilla fragment, left/right di, dm2, m1	1952	Trans. Mus. Mem. 9: 81, 122, 128

SK 840	Left M_3	1952	Trans. Mus. Mem. 9: 112
SK 841a	Juvenile fragmented mandible, left dm2, m1	1952	Trans. Mus. Mem. 9: 140
SK 841b	Right M_3	1952	Trans. Mus. Mem. 9: 112
SK 842	Left dm_2	1952	Trans. Mus. Mem. 9: 140
SK 843	Adolescent left corpus mandible M1-M3	1952	Trans. Mus. Mem. 9: 101, 107
SK 844	Corpus mandible M2-M3	1952	Trans. Mus. Mem. 9: 112
SK 845	Crushed snout, left I2-M2, right I^1, P3-M1	1952	Trans. Mus. Mem. 9: 55, 60, 107
SK 846			
SK 847			
SK 848			
SK 849	Right M^1	1949	unpublished
SK 850	Right P_3	1949	unpublished
SK 851	Right M_3	1952	unpublished
SK 852	Juvenile mandible, left dm1-2, right dm1-2, M1	1952	
SK 853	Lumbar vertebra	1952	Robinson 1972: 101, 113-116
SK 854	Axis	1952	Robinson 1972: 101, 113-116
SK 855	Right M_3	1952	unpublished
SK 856	Right P^4, M^1	1952	unpublished
SK 857	Right P_3	1952	Trans. Mus. Mem. 9: 69-71
SK 858	Mandible, left I^1-M2, right I^1-M3	1952	Trans. Mus. Mem. 9: 35, 36, 101, 107
SK 859			
SK 860	Distal end of humerus	1952	unpublished
SK 861	Mandible fragment, left M1-2	1952	unpublished
SK 862	Mandible fragment, right M1 roots, M2-3	1952	unpublished
SK 863	Fragment $\underline{M}$ crown	1952	unpublished
SK 864	M_1(?) fragment	1952	unpublished

SK 865	Worn, crushed teeth	1952	unpublished
SK 866	Teeth fragments in breccia	1952	unpublished
SK 867	P^3 fragment	1952	unpublished
SK 868	Right M^2, M^3	1952	unpublished
SK 869	Juvenile mandible, fragment roots dml	1952	unpublished
SK 870	Left M^3 fragment	1952	unpublished
SK 871	Left M_3	1952	unpublished
SK 872	Left M^1	1952	unpublished
SK 873	Incisor fragment	1952	unpublished
SK 874	Crown fragment	1952	unpublished
SK 875	Crown fragment	1952	unpublished
SK 876	Mandible fragment, left C root, P3-M3, right I2-M3	1952	unpublished
SK 877			
SK 878	Two teeth and fragment calotte	1952	unpublished
SK 879	Four teeth fragments and associated bone fragments	1952	unpublished
SK 880	Right M_3 and 2 broken teeth	1952	unpublished
SK 881			
SK 882			
SK 883	Right M_3 and associated angle of mandible	1952	unpublished
SK 884	Right $\overline{C}$ and associated mastoid region	1952	unpublished
SK 885	Left M_3 associated with several broken teeth	1952	unpublished
SK 1512	Palatal fragment and teeth	1969	Nature 225: 1114
SK 1514	Mandibular fragment with roots	1969	Nature 225: 1114
SK 1524	Left M^3	1969	Nature 225: 1114
SK 1585	Cranial endocast of subadult	1966	Nature 225: 1114

SK 1586	Robust mandible, right I^{1-2}, M1-3, left I^1, M1-2	1965	Nature 225: 1114
SK 1587a	Left corpus mandible fragment P4, M1	1966	Nature 225: 1114
SK 1587b	Isolated right M_2 belonging to SK 1587a	1966	Nature 225: 1114
SK 1588	Left corpus mandible P4-M1	1966	Nature 225: 1114
SK 1589	Right P^4	1966	Nature 225: 1114
SK 1590	Two palatal fragments, right worn I2-M1, head of femur, and parts of an innominate	1965	Nature 225: 1114
SK 1591	Left M^1	1969	Nature 225: 1114
SK 1592	Palatal fragment with roots of molars	1969	Nature 225: 1114
SK 1593	Right P_3 worn	1966	Nature 225: 1114
SK 1594	Right M_1	1966	Nature 225: 1114
SK 1595	Fragment maxilla, left dm2	1969	Nature 225: 1114
SK 1596	$\underline{C}$ worn	1969	Nature 225: 1114
SK 1648	Anterior part of mandible, right M1-2 worn, left M1	1966	Nature 225: 1114
SK 3155b	Adolescent nearly complete ilium except for anterior superior iliac spine with acetabular portions of ischium and pubis		Day (1973): 33-34
SK 3974	Right M_1 crown	1967	Nature 225: 1114
SK 3975	Left M^3	1967	Nature 225: 1114
SK 3976	Left M_2	1967	Nature 225: 1114
SK 3977	Right M^3	1967	Nature 225: 1114
SK 3978	Infant mandible lacking rami, left dm1-2, right dm1-2, unerupted left M1	1967	Nature 225: 1114
SK 3981a	Last thoraic vertebra	1968	Nature 225: 1114
SK 3981b	Last lumbar vertebra	1968	Nature 225: 1114

SK 14000	$\underline{M}$	1967	Nature 225: 1114
SK 14001	Left P^3	1967	Nature 225: 1114
SK 14003	Part of crushed skull, left M^1, right M1-3	1969	Nature 225: 1114

STERKFONTEIN

STS 1	Adult palate, left $P^3 \rightarrow M^2$, right $P^3 \rightarrow M^1$	1947	Trans. Mus. Mem. 9
STS 2	Juvenile snout with dm1-dm2, fragmentary maxilla with right dm1-dm2	1947	Trans. Mus. Mem. 4
STS 3	Right $\bar{c}$	1947	Trans. Mus. Mem. 9: 44
STS 4	M_2	1947	unpublished
STS 5	"Mrs. Ples" adult female, virtually complete cranium without teeth	1947	Nature 159: 672
STS 6	M_1 and M_2 probably belonging to STS 5	1947	Trans. Mus. Mem. 9: 110
STS 7	Old male mandible with dentition, scapula, proximal humerus	1947	Nature 160: 430
STS 8	Fragmentary maxilla $M^1 \rightarrow M^3$	1947	Trans. Mus. Mem. 9: 48
STS 9	Right M_1	1947	Trans. Mus. Mem. 9: 104
STS 10	Fragmentary maxilla M^2, M^3	1947	unpublished
STS 11	Left M^1, M^2	1947	unpublished
STS 12	Fragmentary maxilla, left $P^3 \rightarrow M^3$, right $P^4 \rightarrow M^2$	1947	Trans. Mus. Mem. 9: 57
STS 13	Snout with right dentition and part of left dentition, elderly adult	1947	unpublished
STS 14	Adult female, 9 thoracic, lumbar, sacrum, l/r innominates, proximal femur	1947	Trans. Mus. Mem. 4: 58-63
STS 16	$\underline{M}$	1947	unpublished
STS 17	Adult female fragmentary cranium with parietal, palate, left P3 → M1 and right P4 → M3	1947	Trans. Mus. Mem. 4: 24-25
STS 18	Juvenile mandible, left dm1, m1, dm2, right m1 → m2	1947	Trans. Mus. Mem. 9: 104
STS 19	Cranial base of STS 58	1947	Trans. Mus. Mem. 4: 27-33

STS 20	Fragmentary calvaria and endocranial cast	1947	unpublished
STS 21	Right M^2	1938	Trans. Mus. Mem. 9: 84
STS 22	Left M^1, M^2	1947	Trans. Mus. Mem. 9: 88
STS 23	Right M^2	1947	unpublished
STS 24	Juvenile male? mandible with deciduous dentition	1948	Trans. Mus. Mem. 4: 42-43
STS 25	Inc. braincase	1948	unpublished
STS 26	Adult female? fragmentary cranium, left maxilla with M^3	1948	unpublished
STS 27	Fragmentary maxilla, left $P^3 \rightarrow M^3$ right $P^4 \rightarrow M^2$	1948	unpublished
STS 28	Right M^2, M^3, left M_1	1948	Trans. Mus. Mem. 9
STS 29	Adult palate M2 → M3	1948	unpublished
STS 30	P^4, M^2	1948	Trans. Mus. Mem. 9: 62
STS 31	M^3	1948	unpublished
STS 32	Fragmentary maxilla $M^2 \rightarrow M^3$	1948	Trans. Mus. Mem. 9: 88
STS 33	$\underline{P}$	1948	Trans. Mus. Mem. 9
STS 34	Right distal femur	1948	Ann. Trans. Mus. 21: 181-182
STS 35	Fragmentary maxilla, left $P^3 \rightarrow M^2$	1948	unpublished
STS 36	Adult male? mandible, worn dentition	1948	AJPA 7: 123-127
STS 37	Left M^2, M^3	1948	Trans. Mus. Mem. 9: 88, 93
STS 38	Fragmentary mandible with RM_3	1948	unpublished
STS 39	Left P^4, M^1	1948	unpublished
STS 40	Fragmentary $\overline{c}$	1948	unpublished
STS 41	Mandible with left M_3	1948	Trans. Mus. Mem. 9: 114
STS 42	Adult palate, Right $P^3 \rightarrow M^3$	1948	Trans. Mus. Mem. 9: 58, 62
STS 43	$\overline{M}$	1948	unpublished

STS 44	Left M^2, M^3	1948	unpublished
STS 45	Fragmentary $\underline{M}$	1948	unpublished
STS 46	M^3	1948	unpublished
STS 47	P^3	1949	Trans. Mus. Mem. 9: 58
STS 48	Left $\underline{C}$	1949	Trans. Mus. Mem. 9: 44-45
STS 49	Fragmentary P_3	1949	unpublished
STS 50	Unerupted left $\bar{c}$ from TM 1516	1936-38	Trans. Mus. Mem. 2: 65
STS 51	Right P_3, left $\bar{c}$	1949	Trans. Mus. Mem. 9: 48, 71
STS 52	Adult female (?) snout with maxillae and upper dentition	1949	Trans. Mus. Mem. 9
STS 52b	Mandible with dentition lacking ramus	1949	Trans. Mus. Mem. 9
STS 53	Adult palate, post-canine dentition	1949	Trans. Mus. Mrm. 9: 88, 93
STS 54	Right M^3	1949	Trans. Mus. Mem. 9: 93
STS 55	P^3	1949	Trans. Mus. Mem. 9: 58
STS 55b	Left M_3	1949	Trans. Mus. Mem. 9: 114
STS 56	M^1, M^2, dm2	1949	Trans. Mus. Mem. 9: 84, 88
STS 57	Fragmentary maxillae, left $MP^3 \rightarrow M^1$	1949	Trans. Mus. Mem. 9: 84
STS 58	Adult calvaria of STS 19	1947	Trans. Mus. Mem. 4: 27-33
STS 59	Left M_3	1949	unpublished
STS 61	Fragmentary maxilla, $P^3 \rightarrow M^2$	1949	unpublished
STS 62	Fragmentary mandible with worn C	1949	unpublished
STS 63	Elderly adult, fragmentary face with orbit and some teeth	1949	unpublished
STS 64	Old adult palate, some teeth	1949	unpublished
STS 65	Right innominate, fragmentary pubis, left proximal femur, fragmentary certebral centrim	1949	Trans. Mus. Mem. 4: 58-63 Day (1973): 33

STS 66	Maxilla and palate, fragmentary dentition	1949	unpublished
STS 67	Fragmentary calvaria, associated M^3	1949	unpublished
STS 68	Proximal radius	1949	unpublished
STS 69	Fragmentary maxilla with some teeth	1949	unpublished
STS 70	Juvenile maxilla, deciduous dentition	1949	unpublished
STS 71	Fragmentary left side of calvaria, adult "skull 7"	1947	Broom *et. al.* (1950): 26
STS 72	Right M^3	1947-49	unpublished

B. The Evidence from East Africa

STERKFONTEIN

Middle Breccia
"Extension Site"

SE 255	Juvenile maxilla M^1, dm^2, dm^1	1957	South Africa Archeol. Bull. 17: 102.
SE 1502	Right M^2	1957	South Africa Archeol. Bull. 17: 102.
SE 1579	Left $M^{1/2}$	1957	South Africa Archeol. Bull. 20: 187.
SE 1937	Left $\bar{c}$	1958	South Africa Archeol. Bull. 17: 102.
SE 2396	Fragment left P^3	1958	South Africa Archeol. Bull. 20: 187.
SE 2398	Post-canine teeth, vertebra	1958	unpublished

TRANSVAAL MUSEUM SPECIMENS FROM STERKFONTEIN AND KROMDRAAI

TM 1511	Holotype Plesianthropus transvaalensis; young adult male cranium with occipital, maxillae, right $P^4 \rightarrow M2$, left $P3 \rightarrow M2$	1936	Nature 138: 486
TM 1512	Maxilla, M3 adult female right maxilla $I2 \rightarrow M1$	1936	Ann. Trans. Mus. 19: 339-373
TM 1513	Distal left femur	1936	Trans. Mus. Mem. 2: 73-75
TM 1514	Old adult male? left maxilla, M^3	1936	Trans. Mus. Mem. 9: 49-50
TM 1515	Old adult male? mandible left $P_3 \rightarrow M_2$	1936-38	Trans. Mus. Mem. 2: 54
TM 1516	Juvenile symphysis, unerupted 1/RC	1936-38	Trans. Mus. Mem. 2: 53
TM 1517 (Kromdraai)	Left cranium, teeth and postcranial bones, holotype Paranthropus robustus	1938	Trans. Mus. Mem. 2: 84-118
TM 1518	Right M_3	1938	Ann. Trans. Mus. 19: 339-373
TM 1519	Worn right M_3	1938	Trans. Mus. Mem. 2: 67
TM 1520	Worn left M_3	1938	Trans. Mus. Mem. 2: 67
TM 1522	Ramus mandible	1936-38	unpublished
TM 1523	Left P_4	1938	Ann. Trans. Mus. 19: 339-373
TM 1524	Root M^1	1938	unpublished
TM 1526	Capitate	1936	Trans. Mus. Mem. 2: 73-75
TM 1527	Right $\underline{C}$	1938	Trans. Mus. Mem. 2: 57
TM 1528	Fragment right C	1938	Ann. Trans. Mus. 19: 339
TM 1532	Left M^3	?	unpublished
TM 1534	Worn $\overline{I}$	1938	unpublished
TM 1535	Upper canine of TM 1514	1938	Trans. Mus. Mem. 9: 56
TM 1536 (Kromdraai)	Juvenile female? mandible deciduous dentition	1941	Nature 147: 607

TM 1561	Right M^3	1938	Trans. Mus. Mem. 2: 57
TM 1600 (Kromdraai)	Mandible fragment, left P_3, M_2, M_3	1954	unpublished
TM 1601 (Kromdraai)	dm_1, $\bar{c}$, P_3, P_4, M^1	1954	unpublished
TM 1602 (Kromdraai)	Fragmentary right maxilla, M^1–M^3	1938?	unpublished
TM 1603 (Kromdraai)	Left M^3 from TM 1517	1944	Trans. Mus. Mem. 9: 92
TM 1604 (Kromdraai)	dm_2	1955	unpublished
TM 1605 (Kromdraai)	Ilium, part of acetabulum, lacking iliac crest	1954	unpublished
TM 3601	Distal femora with broken femoral condyles	?	Day 73: 37-38

AUSTRALOPITHECINE REMAINS FROM MAKAPANSGAT LIMEWORKS

NUMBER	FRAGMENT	DATE DISCOVERY	DESCRIPTION
MLD 1	Calvaria	1947	AJPA (1948) 6: 259
MLD 2	Adolescent mandible	1948	AJPA (1948) 6: 301
MLD 3	Parietal fragment	1948	AJPA (1949) 7: 187
MLD 4	Left M3 isolated	1948	AJPA (1949) 7: 203
MLD 5	Right M2 isolated	1948	AJPA (1949) 7: 201
MLD 6	Cranio-facial fragment ("1st palate")	1948	AJPA (1949) 7: 187
MLD 7	Left ilium	1948	AJPA (1949) 7: 301
MLD 8	Right ischium	1948	AJPA (1949) 7: 301
MLD 9	Premaxillo-maxillary fragment ("2nd palate")	1948	AJPA (1949) 7: 335
MLD 10	Biparieto-occipital fragment	1948	Zeitschr. f. Morphol. u. Anthropol., 1955
MLD 11	Part of infant maxilla	1949	undescribed
MLD 12	Right M3 isolated	1949	undescribed
MLD 13	Isolated upper C	1949	undescribed
MLD 14	Humeral right shaft fragment	1949	L'Anthropol., 1955
MLD 15	Distal right extr. radius	1949	L'Anthropol., 1955
MLD 16	Proximal right extr. radius	1949	L'Anthropol., 1955
MLD 17	Head of femur	1949	L'Anthropol., 1955
MLD 18	Adult mandible	1953	AJPA (1954) 12: 313
MLD 19	Left M3 and mandibular fragment	1955	AJPA (1962) 20: 269
MLD 20	Acrom. extr. right collar bone	1955	undescribed
MLC 1	Right M1 and 2 maxillary fragment	1955	Nature
MLD 21	Very fragmentary ilium	1955	unpublished

NUMBER	FRAGMENT	DATE DISCOVERY	DESCRIPTION
MLD 22	Left fragment mandible, $M_2 \rightarrow M_3$ and sockets of $M_1 \rightarrow P_3$	1953	AJPA (1962) 20(3): 269
MLD 23	Very fragmentary left maxilla with I^2, P^3 same as MLD 6	1955	unpublished
MLD 24	Left M_2	1956	AJPA (1962) 20(3): 269
MLD 25	Juvenile left ilium	1956	AJPA (1958) 16: 473
MLD 26	Fragmentary frontal	1956	undescribed
MLD 27	Symphyseal region of mandible, sockets of incisors and canines and roots of P_3	1956	AJPA (1962) 20(3): 269
MLD 28	Fragmentary right maxilla with palate M^2, M^3	1956	undescribed
MLD 29	Symphyseal region of mandible with fragment of left horizontal ramus	1956	AJPA (1962) 20(3): 269
MLD 30	Associated piece with MLD 11	1949	Trans. Mus. Mem. 9: 28, 45, 59, 63
MLD 31	Right temporal, mastoid, tympanic	1956	undescribed
MLD 32	Proximal extr. left radius	1956	undescribed
MLD 33	Fragmentary right parietal (?), possibly cercopithecoid	1956	undescribed
MLD 34	Right one-half of horizontal ramus of mandible with roots of $M_1 \rightarrow M_2$	1960	AJPA (1962) 20(3): 269
MLD 35	Frag. infant ilium (?)	?	undescribed
MLD 36	Left acromial extr. clavicle	1960	undescribed
MLD 37/38	"Makapansgat skull" adult female cranium, fragmentary maxillae with right $M^1 \rightarrow M^3$ and left M^2	1958-59	AJPA (1962) 20(2): 119
MLD 39	Right distal humerus	1958	Nature (1962) 191: 372
MLD 40	Fragmentary left mandible with $C \rightarrow M_2$	1961	AJPA (1962) 20(3): 269

OLDUVAI GORGE

Geology

Discovered and initially geologically explored by Hans Reck (1914), Olduvai Gorge represents a series of deposits ranging from 2.4 million years to recent times.

The earliest fossiliferous deposit, Bed I, overlies an ashflow tuff termed the Naabi Ignimbrite (Hay, 1971) and is about 30-50 meters thick in the western part of the gorge. In this deposit the major fossil vertebrates and hominid occupation sites have been discovered. Bed I is divided into three members, lower, middle and upper; tuffs of the lower and middle members yield K/Ar ages between 2.03 and 1.91 million years and represent the type occurrence of the Olduvai Normal Event of the Matuyama Reversed Epoch.

The upper member overlies the basalt member, is some 10-40 meters in thickness, and is composed of two units capped by a tuff (Marker Bed B). The upper member contains vertebrate fossils and hominid occupation sites.

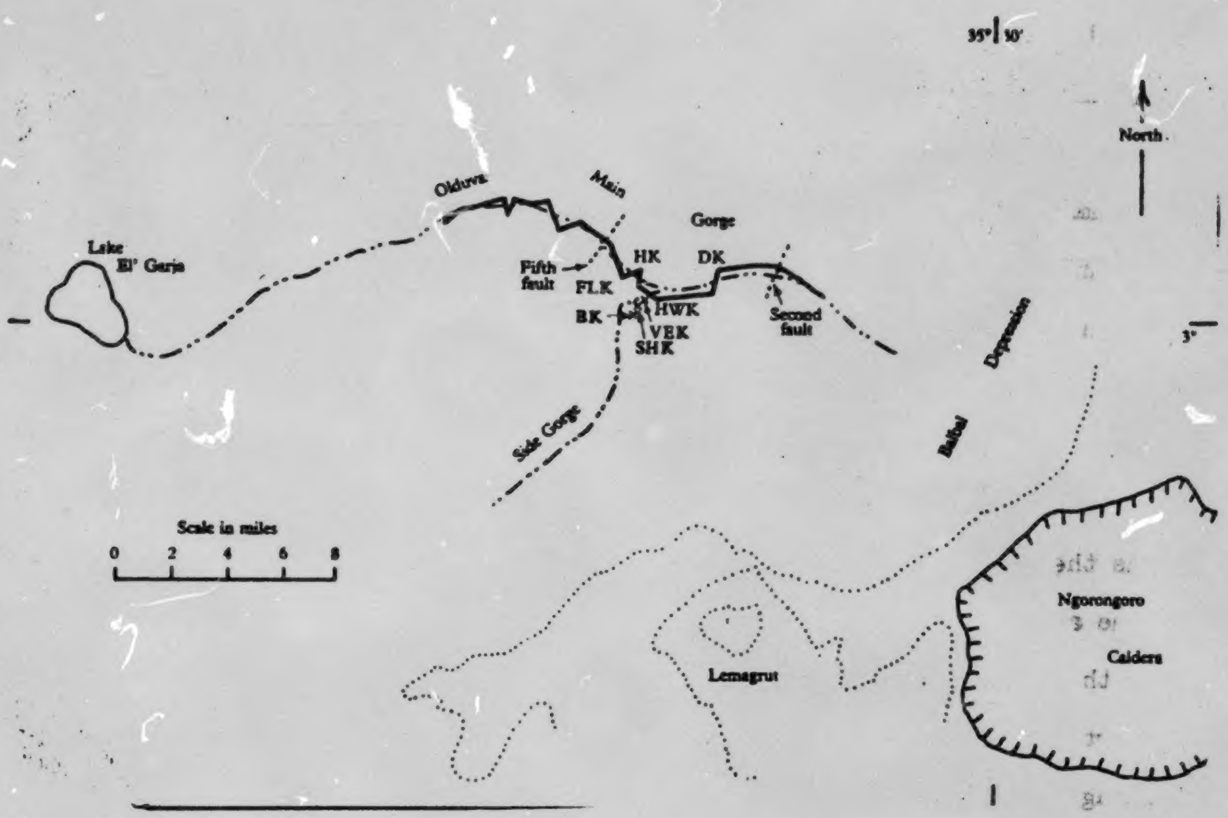
Bed I contains at least six principal tuffs termed Tuffs I^A - I^F. Tuffs I^A to I^E are within the tuff unit of the upper member and Tuff I^F is the capping tuff of Bed I.

The upper deposits of Bed I represent the contractions and expansions of a saline lake; the fossiliferous beds were deposited along low lying terrain to the southeast alternately flooded and dried by seasonal or longer-term climatic changes. Tuffs of the upper member have been dated, with Tuff I^B yielding a mean age of about 1.79 million years. Pumice from the same tuff yielded a fission track age of 2.0 ± 0.25 million years (Fleischer et. al., 1965). Other tuffs above I^B yield similar ages indicating rapid accumulation of the deposit, possibly of the order of 25-50,000 years.

Bed I is overlain by Bed II, the lower part of which is lithologically similar to the upper part of Bed I. Biostratigraphically the upper member of Bed I and the lower part of Bed II can be considered similar. Formerly recognized as the aeolian tuff member (= Lemuta Member of Bed II, Hay 1971) overlays lower Bed II. Four tuffs are interspersed in Bed II termed Tuffs II^A to II^D (oldest to youngest). Tuff II^A is the lowest unit within the Lemute member. The most reasonable K/Ar radiometric determination is 1.71 million years for Tuff II^A. Paleomagnetic studies indicate a change from normal remanent magnetization in lower Bed II to reversed remanent magnetization at the top of the Lemuta member (Grommé and Hay, 1971).

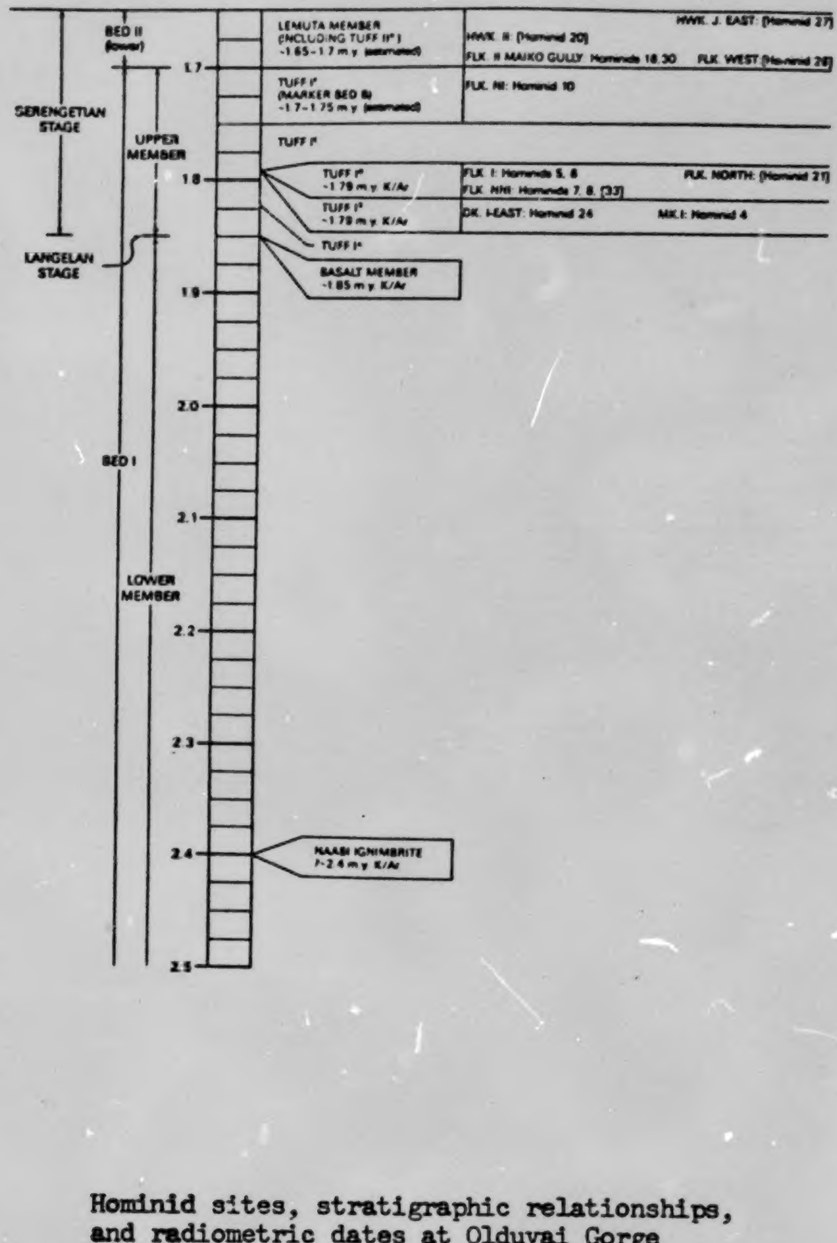
The upper part of Bed II disconformably overlies the earlier deposits as the result of faulting, which reduced the area of the lake and increased the area of surrounding grasslands. Rather abrupt faunal change resulted with animals closely associated to the water decreasing in number. The upper part of Bed II as well as Beds III and IV have been termed the hemagrutian stage by Hay (1967b).

Figure II - 8


35° | 10'
North
Olduvai
Main
Gorge
Lake
El' Garja
Fifth fault
HK
DK
FLK
BK
HWK
VEK
SHK
Second fault
Side Gorge
Balbal
Depression
3°
Scale in miles
0
2
4
6
8
Ngorongoro
Caldera
Lemagrut

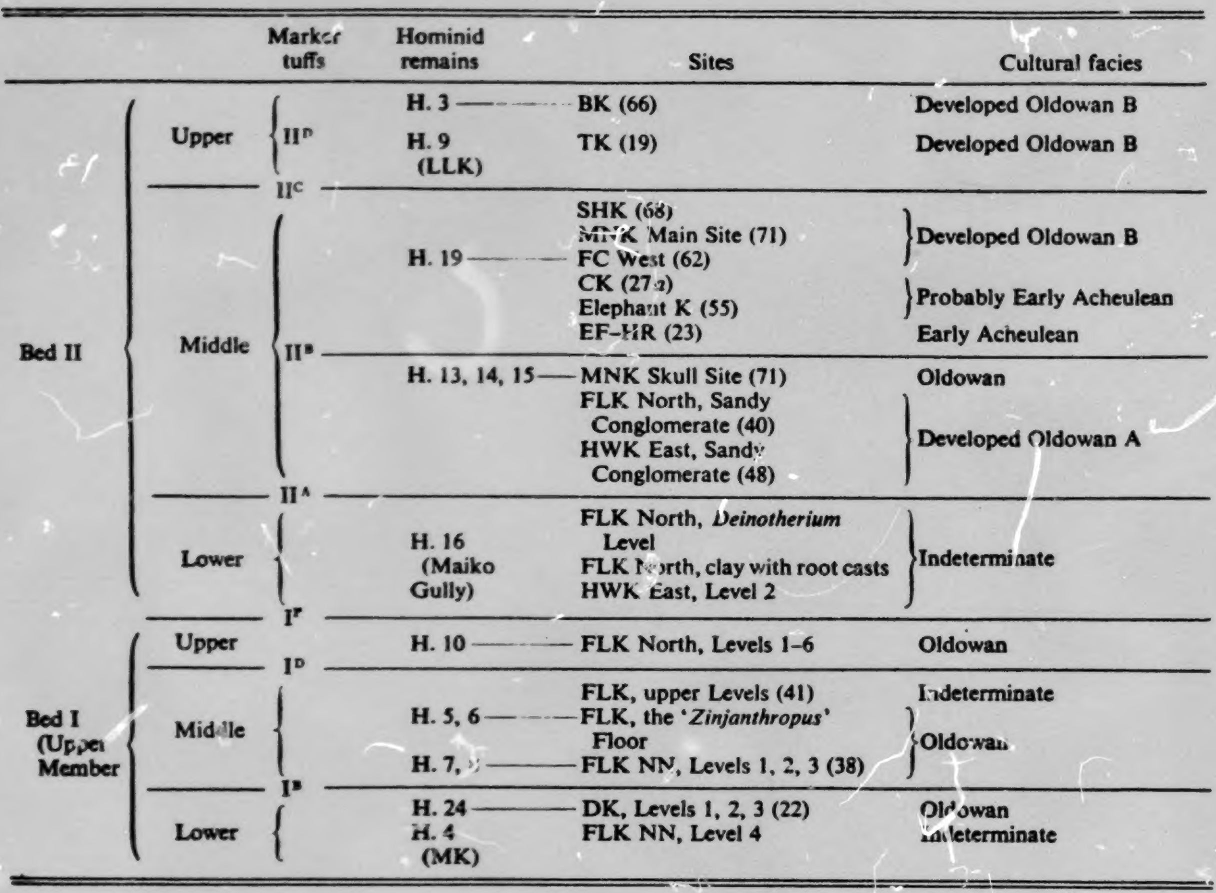
Site plan of the main and side gorges at Olduvai locating hominid sites. (From L. Leakey, Olduvai Gorge Vol I:95)

Figure II - 9


BED II (lower)
SERENGETIAN STAGE
LANGELAN STAGE
UPPER MEMBER
LOWER MEMBER
BED I
1.7
1.8
1.9
2.0
2.1
2.2
2.3
2.4
2.5
LEMUTA MEMBER (INCLUDING TUFF II^{A}) ~1.65–1.7 m.y. (estimated)
TUFF I^{F} (MARKER BED B) ~1.7–1.75 m.y. (estimated)
TUFF I^{E}
TUFF I^{D} ~1.79 m.y. K/Ar
TUFF I^{B} ~1.79 m.y. K/Ar
TUFF I^{A}
BASALT MEMBER ~1.85 m.y. K/Ar
NAABI IGNIMBRITE ?~2.4 m.y. K/Ar
HWK. J. EAST: [Hominid 27]
HWK. II: [Hominid 20]
FLK. II MAIKO GULLY: Hominids 18, 30
FLK. WEST: [Hominid 28]
FLK. NI: Hominid 10
FLK. I: Hominids 5, 6
FLK. NORTH: [Hominid 21]
FLK. NNI: Hominids 7, 8, [33]
DK. I-EAST: Hominid 24
MK.I: Hominid 4

Hominid sites, stratigraphic relationships, and radiometric dates at Olduvai Gorge (Tanzania)
(From Howell (1971):336)

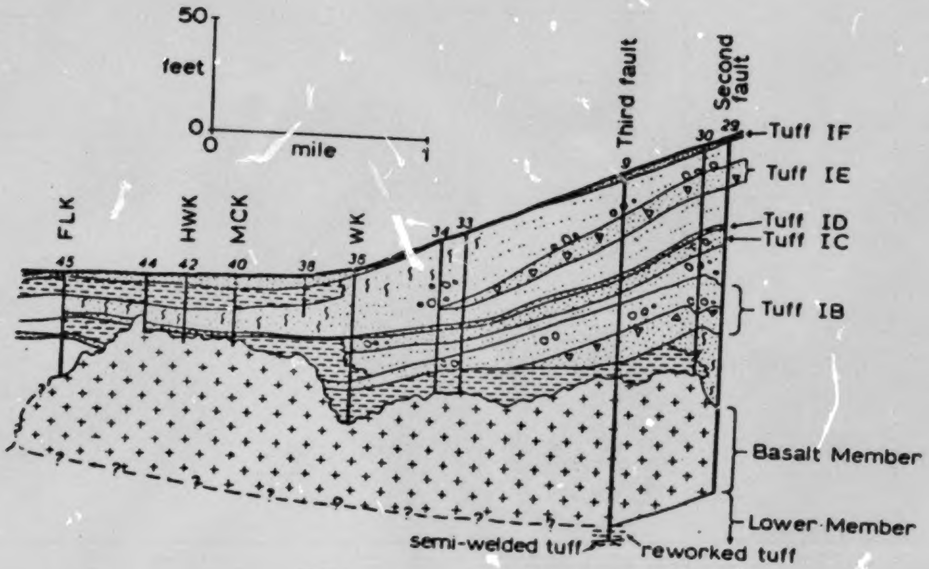
Figure II - 10



		Marker tuffs	Hominid remains	Sites	Cultural facies
Bed II	Upper	II^{D}	H. 3	BK (66)	Developed Oldowan B
			H. 9 (LLK)	TK (19)	Developed Oldowan B
		II^{C}			
	Middle	II^{B}		SHK (68)	Developed Oldowan B
				MNK Main Site (71)	
			H. 19	FC West (62)	
				CK (27a)	Probably Early Acheulean
				Elephant K (55)	
				EF–HR (23)	Early Acheulean
			H. 13, 14, 15	MNK Skull Site (71)	Oldowan
				FLK North, Sandy Conglomerate (40)	Developed Oldowan A
				HWK East, Sandy Conglomerate (48)	
		II^{A}			
	Lower		H. 16 (Maiko Gully)	FLK North, *Deinotherium* Level	Indeterminate
				FLK North, clay with root casts	
				HWK East, Level 2	
		I^{F}			
Bed I (Upper Member	Upper		H. 10	FLK North, Levels 1–6	Oldowan
		I^{D}			
	Middle			FLK, upper Levels (41)	Indeterminate
			H. 5, 6	FLK, the '*Zinjanthropus*' Floor	Oldowan
			H. 7, 8	FLK NN, Levels 1, 2, 3 (38)	
		I^{B}			
	Lower		H. 24	DK, Levels 1, 2, 3 (22)	Oldowan
			H. 4 (MK)	FLK NN, Level 4	Indeterminate

Simplified stratigraphy of Olduvai Gorge
Beds I and II listing hominid remains,
cultural associations and localities.
(From M. D. Leakey, Olduvai Gorge Vol III:3)

Figure II - 11


50
feet
0
0
mile
1
Third fault
Second fault
FLK
HWK
MCK
WK
45
44
42
40
38
35
34
33
30
29
Tuff IF
Tuff IE
Tuff ID
Tuff IC
Tuff IB
Basalt Member
Lower Member
semi-welded tuff
reworked tuff

Diagrammatic cross section of Olduvai Gorge Bed I showing volcanic tuffs and hominid localities.
(From Curtis and Hay (1971): 290)

OLDUVAI GORGE

Fossil Inventory

Found	Number	Site	Description	Published
1913	OH 1	RK II	Burial - complete skeleton	Reck, 1914
1935	OH 2	MNK IV	Parietal fragments	Leakey, 1951: 160
1955	OH 3	BK II	Ldm^2	Leakey, 1958
1959	OH 4	MK I	Homo habilis fragment L. mand. (M_3)	Leakey, Tobias, Napier, 1964
1959	OH 5	FLK I	Australopithecus boisei cranium (Type) palate and upper dentition	Tobias in Leakey, 1967
1959	OH 6	FLK Main	Homo habilis isolated teeth (LM^1, I, LP$_3$)	Leakey, Tobias, Napier, 1964
1960	OH 7	FLK NN I	Homo habilis mandible (Type) (LI, -M_2, RI, -M_1), L/R juv. parietals	Leakey, 1961b
1960	OH 8	FLK NN I	Homo habilis L Pes, 7 tarsals, 5 metatarsals	Day, Napier, 1964
1960	OH 9	LLK II	Homo erectus calvaria	Leakey, 1961
1961	OH 10	FLK N I	Terminal phalange	Day, Napier, 1966
1962	OH 11	DK IV	L maxilla, palate, teeth C-M_2	Tobias et. al., 1965
1962	OH 12	VEK IV	Calotte, palate, teeth P_3-M_2	Leakey, Leakey, 1964
1963	OH 13	MNK II	Calvaria, R maxilla, palate P_3-M_3 mandible, complete dentition distal humeral shaft?	Leakey, Tobias, Napier, 1964
1963	OH 14	MNK II	Juv. calotte parietal, L/R temporal frontal	Leakey, Tobias, Napier, 1964
1963	OH 15	MNK II	Homo sp. isolated teeth (LM^3, RM^3, RC)	Leakey, Tobias, Napier, 1964
1963	OH 16	FLK II Maiko Gully	cf. Australopithecus, 9 cranial frags reconstructed, 10 lower teeth, 11 upper teeth	Leakey, Tobias, Napier, 1964

Found	Number	Site	Description	Published
1963	OH 17	FLK Maiko Gully	Part deciduous, molar	unpublished
1969	OH 18	FLK	Phalanx of hand	unpublished
1963	OH 19	FC II W	upper molar	unpublished
1959	OH 20	HWK II	? A. boisei prox. shaft and neck, L. femur	Day, 1969
1968	OH 21	FLKN	H. Habilis LM^1	Leakey, Clarke Leakey, 1971
1968	OH 22	FLKN	cf. H. erectus, R mandible (P_3-M_2)	unpublished
1968	OH 23	FLK IVb	Homo sp. L mandible (P_4-M_2)	unpublished
1968	OH 24	DKE I	Homo sp. restored cranium	Leakey, Clarke Leakey, 1971
1968	OH 25	Geologic Loc 54, Bed IVa	Frag. left parietal near asterion	unpublished
1969	OH 26	FLK West	RM_3	unpublished
1969	OH 27	HWK I East	H. habilis RM_3	unpublished
1970	OH 28	WK	H. erectus L innominate, L femur	Day, 1971
1969	OH 29	JKW, Beds III - IVa	Frag. molar	unpublished
1969	OH 30	FLK Maiko Gully	Upper teeth: Ldm^{1-2} C-m^1 Rdm^{1-2} C, M^1 Lower teeth: RI_{1-2} LI_1 C_1, M_1	unpublished
1969	OH 31	HWK EI	broken molar	unpublished
1969	OH 32	MNK II	broken molar	unpublished
1969	OH 33	FLK NNI	vault fragments of skull	unpublished
1962	OH 34	JKW III-IVa	H. sp. femur shaft and part of tibia shaft	unpublished
	OH 35	FLK	H. habilis shaft and distal L tibia	unpublished

Found	Number	Site	Description	Published
	OH 36	SC	cf. H. erectus ulna	unpublished
	OH 37	SC	H. sp. fragment L mandible ((M_{1-2}))	unpublished
	OH 48	FLK NN I	cf. australo. clavicle	unpublished
	OH 49	FLK NN	cf. australo. radius shaft	unpublished
	OH 50	FLK NN	rib shaft	unpublished
	OH 43		metatarsals	unpublished

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1971 Further geologic studies and K/Ar dating at Olduvai Gorge and Ngorongoro Crater. In Calibration of Hominoid Evolution, W. Bishop and J. Miller (eds), University of Toronto Press.

Fleischer, R., L. S. B. Leakey, and R. Walker
1965 Fission track dating of Bed I, Olduvai Gorge. Science 148: 72-74.

Experimental procedure is outlined and a date from volcanic pumice taken from site OK I is given at 2.03 ± .28 million years.

Grommé, C. and R. L. Hay
1971 Geomagnetic polarity epochs; age and duration of the Olduvai normal polarity event. Earth and Planetary Science Letters 10: 179-185.

Hay, R. L.
1963 Preliminary notes on the stratigraphy of Beds I through IV, Olduvai Gorge, Tanganyika. Science 139: 829-833.

1967a Hominid-bearing deposits of Olduvai Gorge. In Time and Stratigraphy in the Evolution of Man; Washington: National Academy of Science and National Research Council.

1967b Revised stratigraphy of Olduvai Gorge. In Background to Evolution in Africa, W. Bishop and J. Clark (eds), University of Chicago Press, 221-228.

1971 Geologic background of Beds I and II; stratigraphic summary. In M. Leakey, Olduvai Gorge 3: Excavations in Beds I and II, 1960-1963, Cambridge University Press.

Leakey, L. S. B.
1958 Recent discoveries at Olduvai Gorge, Tanganyika. Nature 181: 1099-1103.

1959a A new fossil skull from Olduvai. Nature 184: 491-493.

Describes a new genus of australopithecine, Zinjanthropus boisei, and on the basis of faunal evidence (which is similar to Omo and to Taungs) claims the age of Bed I, Olduvai, as upper Villafranchian instead of lower Middle Pleistocene.

1959b The first men; recent discovery in East Africa. Antiquity 33.

1960a Finding the world's earliest man. National Geographic 118: 420-435.

1960b The affinities of the Olduvai australopithecine. Nature 186: 458.

Reply to J. T. Robinson (Nature 186: 456-458) concerning the taxonomix status of Zinjanthropus boisei. He agrees that Zinjanthropus is closely related to the australopithecinae but believes the differences are enough to justify separate generic rank from Paranthropus. Claim based on alleged differences in cranium and relatively greater reduction of the canines in comparison with total molar-premolar series.

Leakey, L. S. B.

1961a New finds at Olduvai Gorge. Nature 189: 649-650.

Announces the discovery of additional specimens of fossil hominid at FLK NN I including a hominid mandible as well as parts of two parietals. Age of the specimen estimated at 12 years on the basis of present day tooth eruption. Claims overall dental pattern does not appear to be compatible with Zinjanthropus.

1961b The juvenile mandible from Olduvai. Nature 191: 417-418.

Additional information on the mandible of the juvenile hominid discovered at the site FLK NN I (OH 7). Describes the measurements for the third and fourth lower premolars, the first and second lower molars, and a single upper molar. Believes the juvenile is a very remote and truly primitive ancestor of Homo.

1961c Exploring 1,750,000 years into man's past. National Geographic 120: 564- .

1962 The Olduvai discoveries. Antiquity 36: 119-122.

1963a The makers of the industries at Olduvai and in the South African caves. In African Ecology and Human Evolution, F. C. Howell and R. Bourliere (eds.), New York: Aldine Publishing Company, 598-599.

1963b East African fossil Hominoidea and the classification within this super-family. In Classification and Human Evolution, S. L. Washburn (ed.), New York: Aldine Publishing Company, 32-49.

1965 Olduvai Gorge, volume I. New York: Cambridge University Press, 118 pp.

1966 Homo habilis, Homo erectus and the australopithecines. Nature 209: 1279-1281.

Argues that Homo habilis is distinct from any Australopithecus in many morphological aspects; the U-shaped structure of the australopithecine mandible being the most obvious. He also believes that by Lower Pleistocene times H. habilis, H. erectus, as well as the australopithecines, were all evolving along distinct lines and rejects the idea that the H. habilis represents a stage between A. africanus and H. erectus.

Leakey, L. S. B. and F. C. Howell

1960 The newest link in human evolution; the discovery by L. S. B. Leakey of Zinjanthropus boisei. Current Anthropology 1: 76-77.

Leakey, L. S. B. and M. D. Leakey

1964 Recent discoveries of fossil hominids in Tanganyika: at Olduvai and near Lake Natron. Nature 202: 5-7 (reprinted in Current Anthropology 6: 422-424 (1965)).

Specimens from sites VEK IV (OH 12), MNK II (OH 13), (OH 14), (OH 15); and FLK II Maiko Gully (OH 16) are announced as well as a large australopithecine mandible from Lake Natron by Richard Leakey and Glynn Isaac.

Leakey, L. S. B., Napier, J. R., and Tobias, P. V.
1964 A new species of the genus *Homo* from Olduvai Gorge. Nature 202: 7-9.

> Revised diagnosis of the genus *Homo* to include a new species *Homo habilis*. Differs from australopithecus in cranial capacity of 600+ cc., and lacks concave or dished-in face with smaller molar teeth. Describes the type specimen OH 7 and paratypes OH 13, 8, 6, and 4 and referred material OH 14, 16. Claims contemporaneity with australopithecus.

Leakey, M. D.
1969 Recent discoveries of hominid remains at Olduvai Gorge, Tanzania. Nature 223: 756.

> The nearly complete skull (OH 24) from DK East is preliminarily described. The specimen was discovered in the earliest known fossiliferous horizon. Stone tools were found of the Olduway type in a nearby site. The discoveries of OH 21, 22, 23, 26, and 27 are also announced.

1971 Olduvai Gorge, Volume III. Cambridge, UK: Cambridge University Press.

Leakey, M. D., Clarke, R. J., and Leakey, L. S. B.
1971 New hominid skull from Bed I, Olduvai Gorge, Tanzania. Nature 232: 308-312.

> OH 24 is announced from site DKE I, which differs in some respects from the type of *Homo habilis* from Bed I. A case for sexual dimorphism is made. A complete description of the cranium is made as well as comparisons with *Australopithecus* and *Homo erectus*. Claims that the differences which exist between the type *H. habilis* from Bed I and the paratypes from Bed II are not the result of an elapse of a prolonged time interval.

Napier, J. R.
1961 Human origins: recent discoveries at Olduvai Gorge. Lancet 2: 767-768.

1965 Comments on 'New Discoveries in Tanganyika: Their Bearing on Hominid Evolution' by P. V. Tobias. Current Anthropology 6: 402-403.

Napier, J. R. and Weiner, J. S.
1962 Olduvai Gorge and human origins. Antiquity 36: 41-47, 121-122.

Oakley, K. P.
1959 The first men: recent discovery in East Africa. Antiquity 33: 286-287.

Payne, M. M.
1965 The Leakeys in Africa: family in search of prehistoric man. National Geographic 127: 194-231.

1966 Preserving the treasures of Olduvai Gorge. National Geographic 130: 700-709.

Pilbeam, D.
1970 Early hominids and cranial capacities. Nature 227: 747-748.

On the basis of comparing the cranial capacity of OH 7 with that of other gracile australopithecines, the author does not feel that the specimen should be included in the species A. africanus but rather to another species of the same genus. OH 7 differs as much from earlier hominids as does the gorilla from the chimpanzee.

Reck, H.
1951 A preliminary survey of the tectonics and stratigraphy of Olduvai. In L. S. B. Leakey, Olduvai Gorge, Cambridge University Press, 5-19.

Robinson, J. T. and Leakey, L. S. B.
1959 An alternative interpretation of the supposed giant deciduous hominid tooth from Olduvai. Nature (London) 185: 407-408.

Robinson, J. T.
1960 The affinities of the new Olduvai australopithecine. Nature 186: 456-458. Reprinted in Yearbook of Physical Anthropology, Vol. 9, 1953-1961, 91-95.

Disagrees with L. S. B. Leakey's assertion that Zinjanthropus boisei should be considered generically distinct from Paranthropus. Claims that characteristics such as continuous nuchal crest, enlargement of mastoid area, do not represent a separate difference but are reflections of the fact that this specimen is a little larger in size.

1965a Homo habilis and the australopithecines. Nature 205: 121-124.

1965b Comments on 'New Discoveries in Tanganyika: Their Bearing on Hominid Evolution', by P. V. Tobias. Current Anthropology 6: 403-406.

1966 The distinctiveness of Homo habilis. Nature 209: 957-960.

Acknowledges that some detectable differences between known specimens of Homo habilis and known australopithecines exist but questions the significance of those differences. Recalculates cranial capacities for australopithecines and gives range between 300-550 cm^3. Reiterates his position of maintaining separate generic rank between Paranthropus and A. africanus and proposes lumping australopithecines with genus Homo.

Simons, E., P. Ettel and D. Pilbeam
1969 Controversial taxonomy of fossil hominids. Science 166: 258-259.

Discusses the position of Homo habilis. Claims that the Bed I "habilis" material closely resembles Australopithecus sp. from South Africa and that the evidence favors its placement in that genus. The Bed II "habilis" material differs in size from Bed I and resembles Homo erectus. Reiterates valid objections to the concept "H. habilis" and proposes procedures to be used to assess taxonomic affinities.

Tobias, P. V.

1964 The Olduvai Bed I hominine with special reference to its cranial capacity. Nature 202: 3-4. Reprinted in Current Anthropology 6 (1965): 421-422.

1965a *Homo habilis*: reply to Ashley Montagu. Science 149: 918.

1965b New discoveries in Tanganyika: their bearing on hominid evolution. Current Anthropology 6: 391-411.

1966 The distinctiveness of *Homo habilis*. Nature 209: 953-957.

Defends the validity of the species *Homo habilis*. Examines dental characteristics, inner contour of the mandible, the length/breadth index of molar teeth, and cranial capacity of *Homo habilis* and *Australopithecus*. Recognizes three branches of the australopithecinae, a mesodont branch (*A. africanus*), a macrodont branch (*A. robustus*) and a megadont variant (*A. boisei*).

1967a The cranium and maxillary dentition of *Australopithecus* (*Zinjanthropus*) *boisei*. Olduvai Gorge, Volume II, Cambridge University Press.

1967b General questions arising from some lower and middle Pleistocene hominids of the Olduvai Gorge, Tanzania. South Africa Journal of Science 63: 41-48. Reprinted in Yearbook of Physical Anthropology, 1967, 31-38.

1972 "Dished faces", brain size and early hominids. Nature 239: 468-469.

The author supports the assignment of OH 24 to the genus *Homo*, and explains why, despite arguments that uts cranial capacity is too small and its dished face is more characteristic of australopithecines. No plates or tables.

Tobias, P. V. and von Koenigswald, G. H. R.

1964 A comparison between the Olduvai hominines and those of Java and some implications for hominid phylogeny. Nature 204: 515-518. Reprinted in Current Anthropology 6(1965): 422-424.

Wolpoff, M. H.

1969 Cranial capacity and taxonomy of Olduvai Hominid 7. Nature 223: 182-183.

1970 Taxonomy and cranial capacity of Olduvai Hominid 7 (cont'd). Nature 227: 747.

Reiterates his previous view that OH 7 should be considered as part of the population of South African gracile australopithecines and grouped under the taxonomic rank of *Homo africanus*.

SOUTH WEST LAKE RUDOLF

Three localities of Pliocene/Pleistocene age are located in the Turkana District, Southwest Lake Rudolf, a large basin drained by the Kerio River. Two of the localities, Kanapoi and Lothagam, have yielded hominid fossils in association with assemblages of other vertebrates. The third locality, Ekora, has not as yet produced fossil remains.

The Kanapoi sediments are exposed by dissections of the Kakurio River, a seasonal tributary to the Kerio. The sediments overlie a Miocene surface, are some 65-70 meters in thickness, and are fluviolocustrine in content. Interbedded successive ash falls and substanial deposits of waterlaid tuffs are present. Three radiometric age determinations on an overlying basalt member earlier published produced a minimum age of the Kanapoi sediments overaging 2.7 million years. The lava has as well reversed geomagnetic polarity. Reports of contamination of the basalt and consequent redating of the material has yielded ages between 4 and 4.5 million years. These dates correlate clober with the vertebrate assemblage which is comparable with that of the Mursi Assemblages at Omo of a substantially older age. The single hominid specimen (Kanapoi Hominid 1), represented by the distal end of the left humerus, is therefore of particular interest as the oldest of such remains from this period.

To the northeast of Kanapoi, the Lothagam Hill locality represents isolated exposures of Miocene and Pliocene volcanics dated radiometrically between 16.8 and 8.3 million years overlain by end Tertiary sediments. The Lothagam Group totals over 700 meters in thickness and three principal sedimentary units, Loth gam 1-3, have been recognized. Lothagam 1 is subdivided into three members A-C and a minimum age for this series is taken from an overlying basalt sill yielding a radiometric date of 3.71 million years. The analysis of the lower vertebrate fauna from Lothagam 1 suggest a much older age for the underlying sediments in excess of the Mursi Formation at Omo, perhaps as old as 5 to 5.5 million years.

The single hominid specimen from Lothagam-1 was recovered during the field investigations of the Museum of Comparative Zoology, Harvard University during 1967, together with other vertebrate fossils. The hominid specimen was described as Australopithecus sp. cf. A. africanus and consists of a fragment of the mandibular body with worn M_1, perhaps the oldest known fossil representative of the family Hominidae.

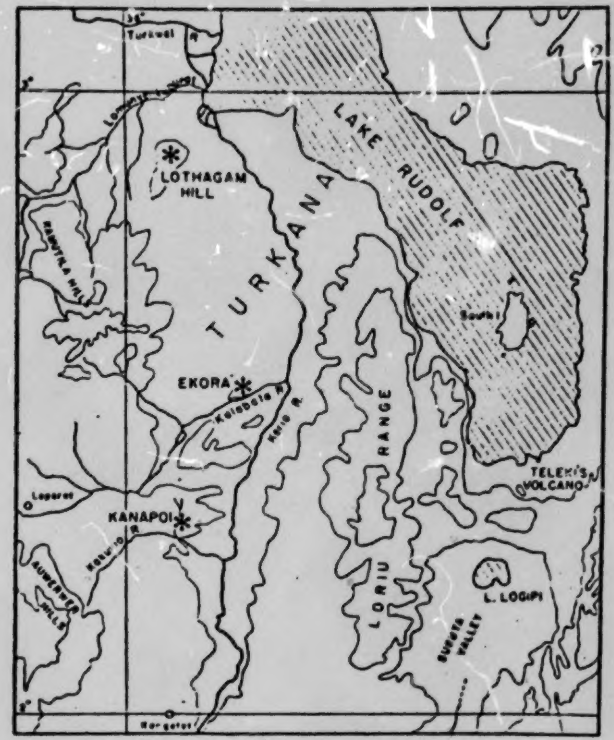
Leakey, M. D.
1966 Primitive artifacts from Kanapoi Valley. Nature 212: 579-581.

Patterson, B.
1966 A new locality for early Pleistocene fossils in northeastern Kenya. Nature 212: 577-578.

Patterson, B. and W. Howells
1967 Hominid humeral fragment from early Pleistocene of northwestern Kenya. Science 156: 64-66.

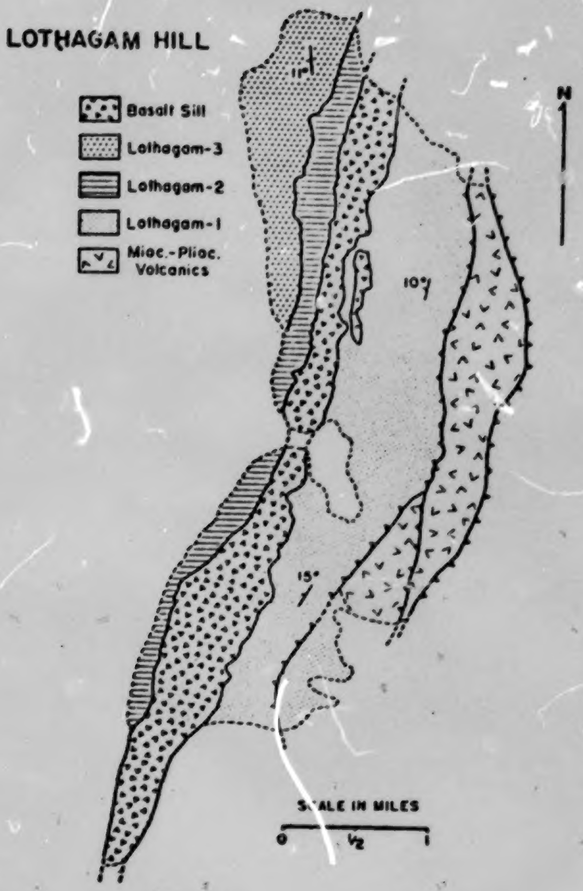
Patterson, B., A. Behrensmeyer and W. Sill
1970 Geology and fauna of a new Pliocene locality in northwestern Kenya. Nature 226: 918-921.

Figure II - 12


36°
Turkwel R.
3°
LOTHAGAM HILL
TURKANA
LAKE RUDOLF
South I.
EKORA
Kalabata R.
Kerio R.
LORIU RANGE
TELEKI'S VOLCANO
Loperot
KANAPOI
Kakurio R.
AUWERWER HILLS
L. LOGIPI
SUGUTA VALLEY
2°

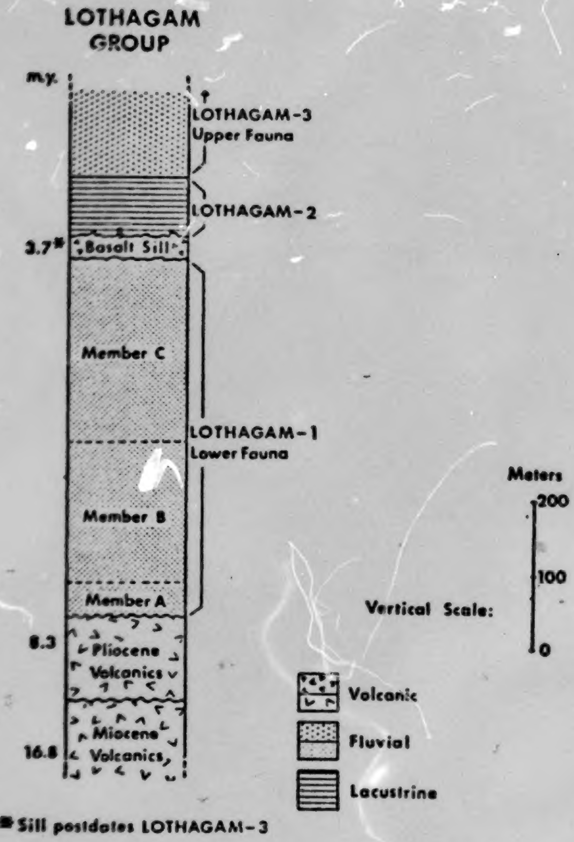
Map of the Southwest Lake Rudolf hominid bearing deposits of Lothagam, Kanapoi and Ekora localities, Kenya.
(From Patterson _et_. _al_. (1970): 919)

Figure II - 13


LOTHAGAM HILL
Basalt Sill
Lothagam-3
Lothagam-2
Lothagam-1
Mioc.-Plioc. Volcanics
N
11°
10°
15°
SCALE IN MILES
0
½
1

Simplified geological map of Lothagam locating deposits listed in columnar section.
(From Patterson et. al. (1970):919)

Figure II - 14


LOTHAGAM GROUP
m.y.
LOTHAGAM-3
Upper Fauna
LOTHAGAM-2
3.7*
Basalt Sill
Member C
LOTHAGAM-1
Lower Fauna
Member B
Member A
8.3
Pliocene Volcanics
Miocene Volcanics
16.8
*Sill postdates LOTHAGAM-3
Meters
200
100
0
Vertical Scale:
Volcanic
Fluvial
Lacustrine

Simplified stratigraphy of the stratigraphy at Lothagam.
(From Patterson et. al. (1970):920)

EAST LAKE RUDOLF

Geochronology

In the eastern region of the Rudolf Basin a series of sediments and lavas of Pliocene/Pleistocene age have been explored since 1968 by an investigating team led by R. E. F. Leakey. The exposures extend from north to south, from the Ileret sector to the Koobi Fora and Kubi Alga sectors near Allia Bay north of Sibilot Mountain. Overall area of the deposits is in excess of 2500 Km^2. The Ileret and Koobi Fora sectors are separated by the Kokoi horst near Lake Rudolf and by the Suregei Plateau to the northeast, both apparently of late Miocene age. Radiometric determination of basalt flows have yielded dates between 11.6 and 14.1 million years. The sediments and associated lavas of the Koobi Fora and Ileret successions near the lakeshore are tilted to the west and cut by parallel faults producing eastern facing fault scarps similar to the situation affecting the Usno and Shungura Formations of the Lower Omo Basin.

The Koobi Fora Formation includes those sedimentary strata which lie between the basal Suregei Tuff Complex and the prominent tuff exposed along the Ileret ridge, the Chari Tuff. This includes the Koobi Fora I, II and III units and the Ileret lower and middle unit as described in Howell (1971). The Ileret member of the Koobi Fora Formation consists of the "lower" and "middle unit" between the contact of the KBS Tuff in the Ileret area and the top of the Chari Tuff capping the whole Koobi Fora Formation. In the Koobi Fora area the lower portion of the formation between the basal contact and top of the KBS Tuff including KF-I and KF-IIa is referred to as the lower member. Strata above the KBS Tuff are referred to as the upper members including KF-IIb through KF-III.

The geological succession of the KoobiFora/ Kubi Alga sectors has been described by Behrensmeyer (1971) and Bowen and Vondra (1973). The earliest deposits (KF-I and the Kubi Alga beds) overlie an erosional volcanic surface and are essentially lacustrine in composition. Rare rolled and broken mammalian fossils suggest a late Pliocene age somewhat in excess of Kanapoi or upper Lothagam. Radiometric determinations for a tuff within the Kubi Alga Beds has yielded an age of 4.5 million years.

The deposits of KF-II are essentially fluviatile and are on the average some 50 meters in thickness. KF-II is divided into earlier (A) and later (B) subunits separated by an extensive pumiceous tuff (KBS Tuff) some 2.5 meters in thickness and composed of both fluviatile and aeolian components. This tuff has previously yielded dates averaging 2.6 million years. The overall composition of the vertebrate fauna, however, suggests much more recent age equivalent to the upper deposits of the Shungura Formation, perhaps 2.0 million years. Recent, as yet, unpublished radiometric determinations of the KBS Tuff by the K/Ar Laboratory of the University of California at Berkeley suggest ages closer to 1.5 million years. The question of the antiquity and significance of the hominid associations must await the resolution of this problem.

Stone artifacts have also been found in association with the tuff along with a mammalian fossil assemblage.

In the upper member, subunit KF-IIb has a maximum aggregate thickness of 30 meters and appears to be composed of alluvial fan deposits. Above this, KF-III is downfaulted some 15 to 25 kilometers inland from the present shores of Lake Rudolf. This unit has an aggregate thickness of over 70 meters and largely reflects deposits of deltaic and shallow lacustrine action. The lower fossiliferous sands of KF-III are overlain by a massive tuff (KF-III tuff) up to 12 meters in thickness which also has yielded vertebrate fossils.

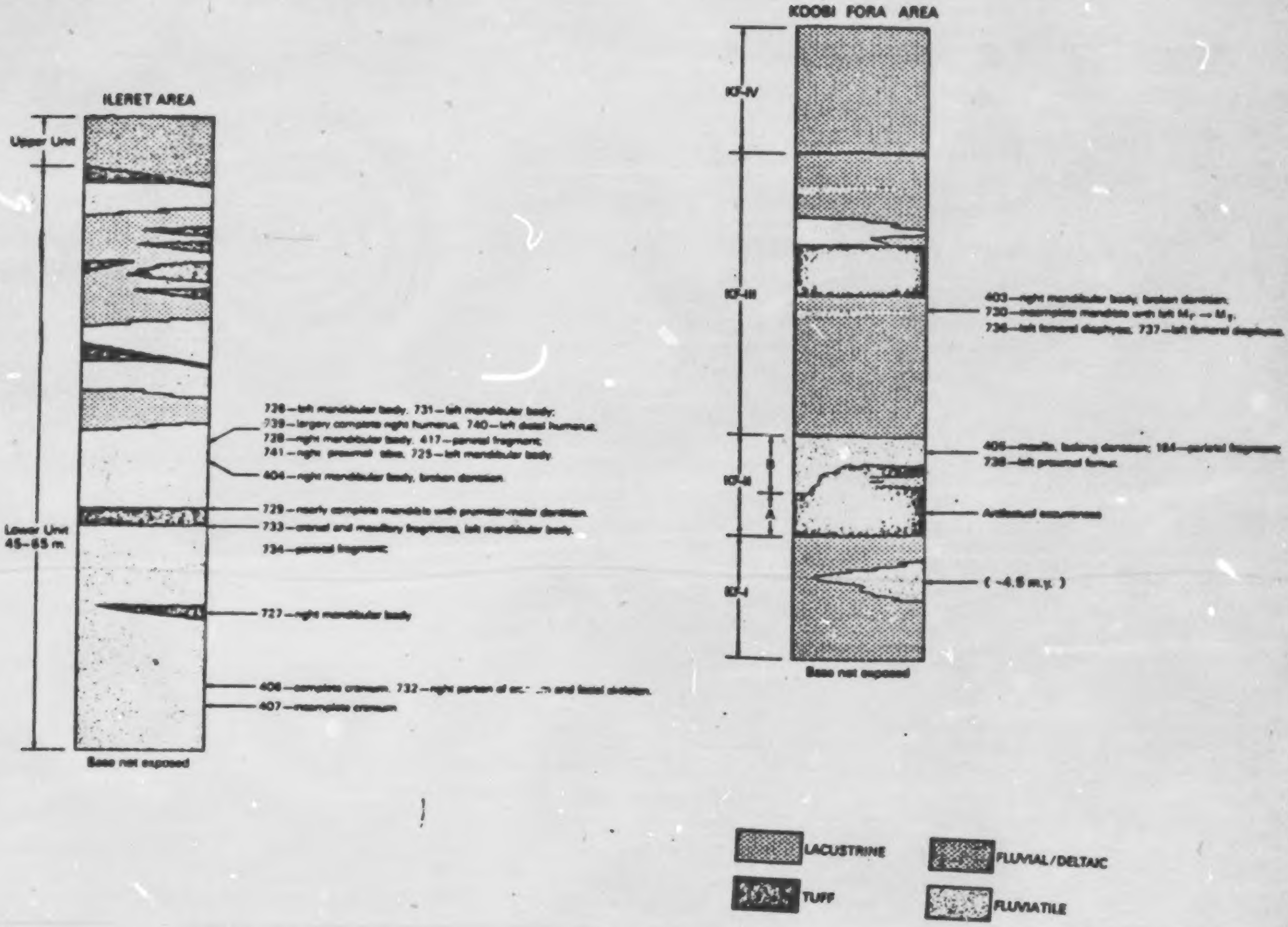
•The Ileret member is extensive in sediments of sandstones and siltstones and lavas. Two faunal zones are represented and hominids have been found associated with both fluviatile and tuff deposits.

The relationship between the Koobi Fora succession and that in the Ileret area is not completely understood. Attempts have been made to trace potential marker horizons between the two areas with some confidence. (Bowen and Vondra 1973: 392).

Those strata which lie below the Suregei Tuff Complex are referred to as the Kubi Alga Formation and are the earliest sediments of the East Rudolf succession.

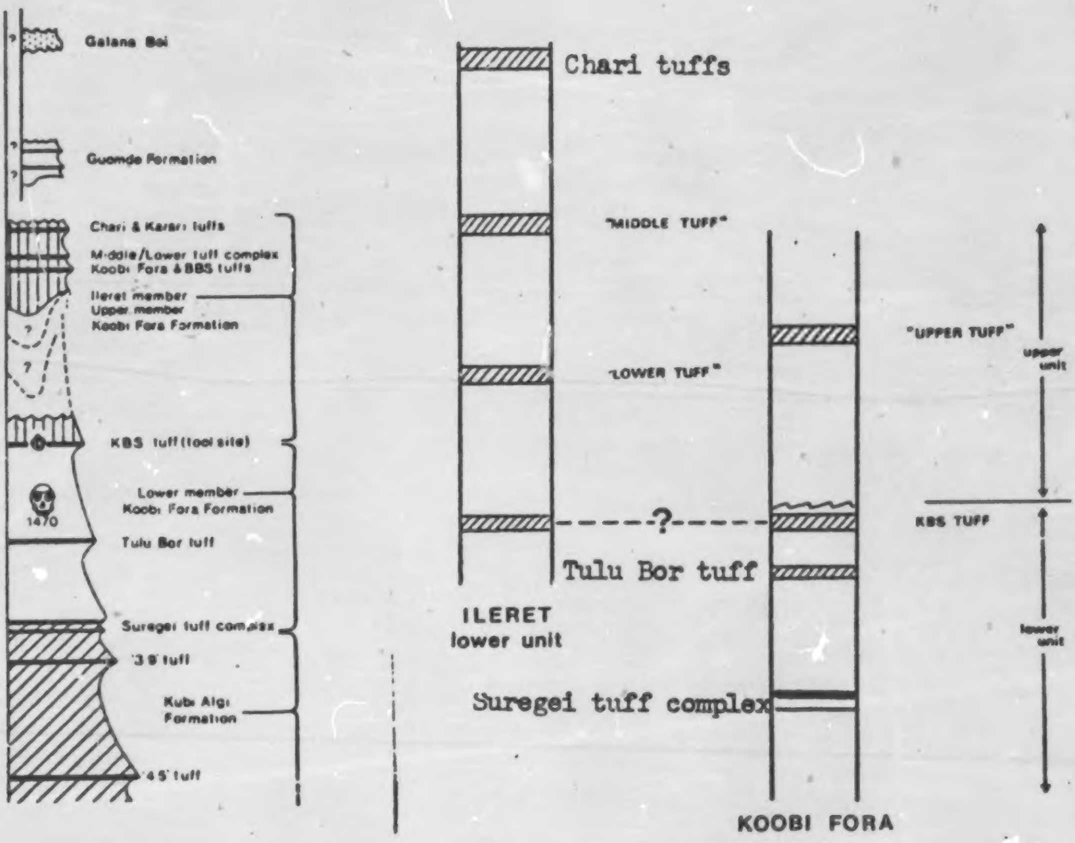
A simplified stratigraphical relationship between the Ileret and Koobi Fora successions is presented in Figure II - 15, 16.

Figure II - 15


ILERET AREA
Upper Unit
Lower Unit 45–65 m.
726—left mandibular body. 731—left mandibular body;
739—largely complete right humerus. 740—left distal humerus.
728—right mandibular body. 417—parietal fragment;
741—right proximal tibia. 725—left mandibular body.
404—right mandibular body, broken dentition.
729—nearly complete mandible with premolar-molar dentition.
733—cranial and maxillary fragments, left mandibular body.
734—parietal fragment.
727—right mandibular body
406—complete cranium. 732—right portion of [illegible] and facial skeleton.
407—incomplete cranium
Base not exposed
KOOBI FORA AREA
KF-IV
KF-III
KF-II
B
A
KF-I
403—right mandibular body, broken dentition.
730—incomplete mandible with left $M_1 \rightarrow M_3$.
736—left femoral diaphysis; 737—left femoral diaphysis.
405—maxilla, lacking dentition; 164—parietal fragment;
738—left proximal femur.
Artifactual occurrence
(~4.5 m.y.)
Base not exposed
LACUSTRINE
FLUVIAL/DELTAIC
TUFF
FLUVIATILE

Simplified stratigraphy and hominid bearing localities in the East Lake Rudolf area. From Howell (1971): 344-345.

Figure II - 16


Galana Boi
Guomde Formation
Chari & Karari tuffs
Middle/Lower tuff complex
Koobi Fora & BBS tuffs
Ileret member
Upper member
Koobi Fora Formation
KBS tuff (tool site)
Lower member
Koobi Fora Formation
1470
Tulu Bor tuff
Suregei tuff complex
'3 9' tuff
Kubi Algi
Formation
'4 5' tuff
Chari tuffs
"MIDDLE TUFF"
"LOWER TUFF"
?
Tulu Bor tuff
ILERET
lower unit
Suregei tuff complex
"UPPER TUFF"
upper unit
KBS TUFF
lower unit
KOOBI FORA

Relationships between the Koobi Fora and Ileret Successions. (Left from Fitch et. al. (1974): 213. Right from Leakey (1972): 265.)

EAST LAKE RUDOLF

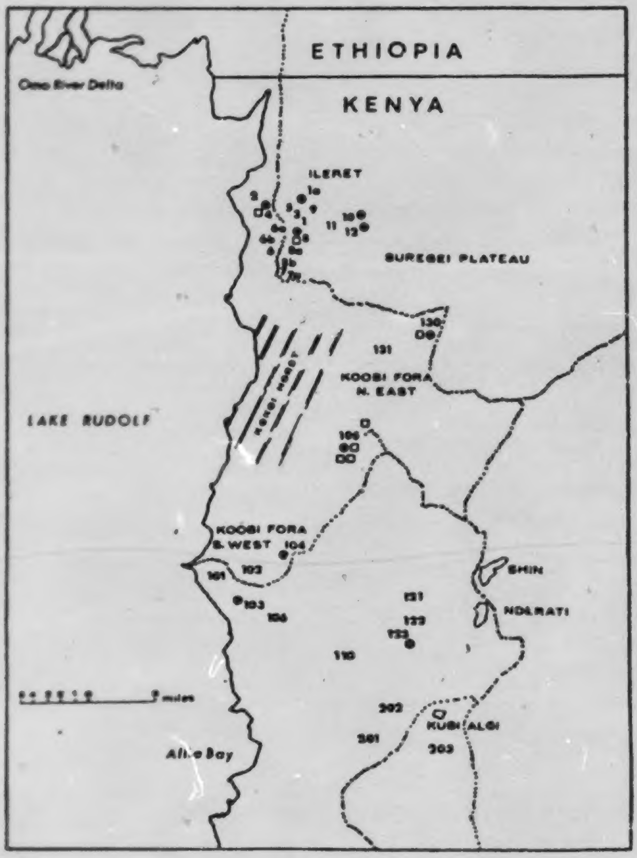
Biochronology

More than 80 hominid specimens have been recovered from the exposures of the East Rudolf Basin. Figure II-17shows the geographic distribution of the collecting localities yielding fauna and artifacts. The three subregions which have been recognized—Kubi Alga, Koobi Fora Ridge and Ileret—have been designated by a numerical reference system for localities: Ileret 1-99. Koobi Fora Ridge 100-199, Kubi Alga 200-299.

An abundant vertebrate fossil assemblage has been collected along with the hominid remains. Several taxa are represented by successive grades of a single evolving lineage and are, therefore, useful for faunal correlation. The three most important species for this purpose are the suids, *Mesochoerus limnetes* and *Metridiochoerus andrewsi*, and the elephant *Elephas recki*. The faunal samples from the East Rudolf deposits have been divided into four assemblages each based on a distinct group of fossil vertebrates, and each being derived from a definable segment of the stratigraphic sequence. Faunal lists are given in Figure II-18; faunal zones and lithostratigraphic units are presented in Figure II-19.

The mean value of samples from the *Mesochoerus limnetes* faunal zone can be compared with material from Member F of the Shungura Formation (Tuffs D-F) in the Lower Omo dated radiometrically at about 2.0 million years. The chronostratigraphic limits are 2.7 million years and 1.8 million years and may be taken as the approximate maximum and minimum indicated age limits for the fauna of the *Mesochoerus limnetes* zone for this species only. Similar indicated mean and maximum age limits for the *Metridiochoerus andrewsi* and *Loxodonta africana* zones are 1.7 million years (1.8 - 1.6 million years) and 1.2 million years (1.4 - 0.9 million years) respectively (Maglio 1972: 384). Comparing,the elephants'and suids' mean indicated ages and suggested limits from the *M. limnetes* zone are 2,5 million years (3.4 - 2.1 million years); from the *M. andrewsi* zone are 1.7 million years (2.1 - 1.4 million years); and from the *L. africana* zone are 1.4 million years (1.7 - 1.2 million years).

Figure II - 17


ETHIOPIA
KENYA
Omo River Delta
ILERET
1a
2
4
3
1
9
10
11
12
6a
8
6b
8a
6
8b
7a
SUREGEI PLATEAU
130
131
KOOBI FORA
N. EAST
LAKE RUDOLF
105
KOOBI FORA
S. WEST
104
102
101
103
106
SHIN
121
NDERATI
123
122
110
miles
202
KUBI ALGI
201
203
Alia Bay

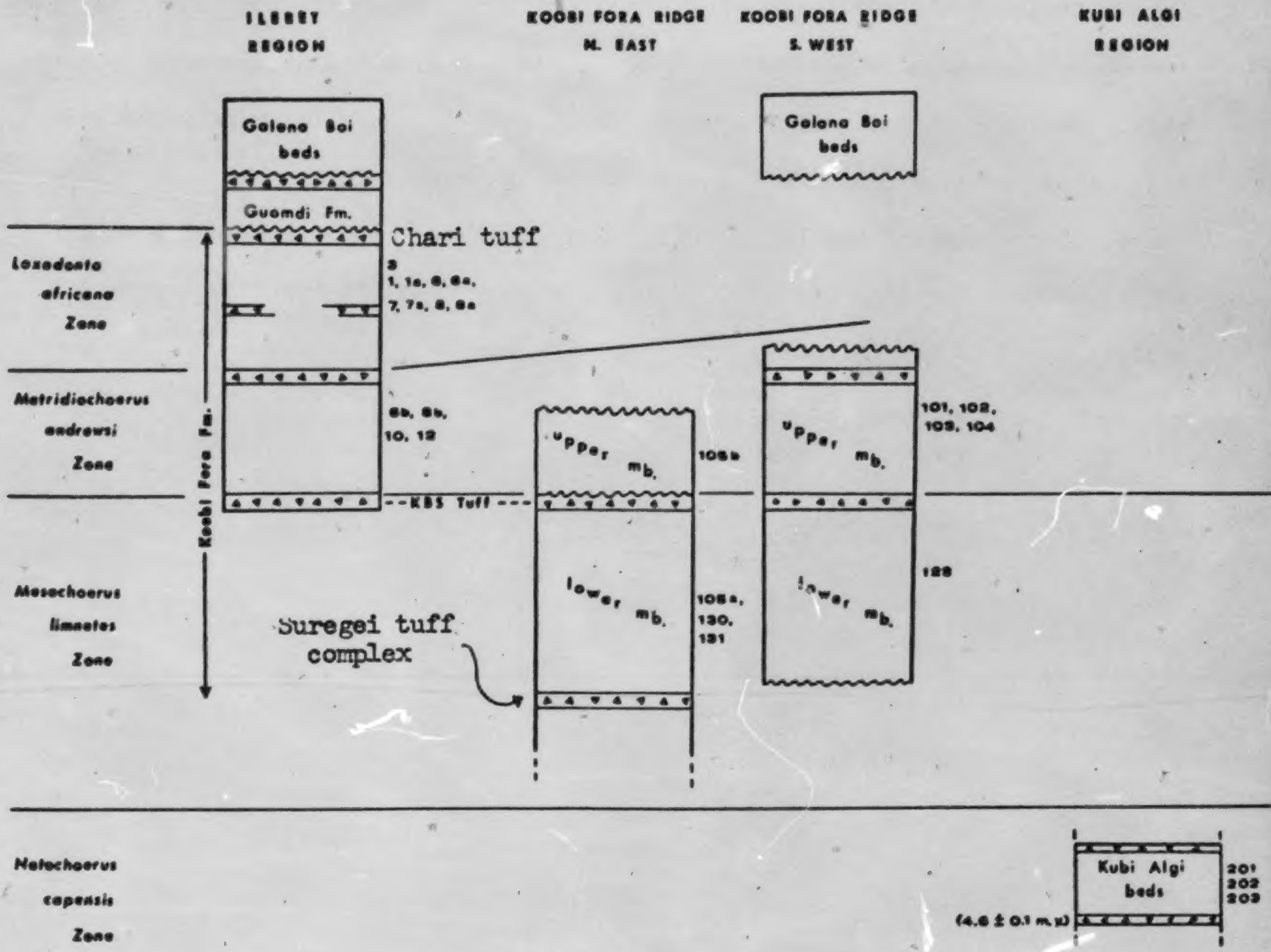
East Lake Rudolf, Kenya. Distribution of principal localities of Pliocene-Early Pleistocene sites. (From Maglio (1972):379)

Figure II - 18

Faunal zone	Areas of occurrence	Geological unit	Diagnosis
Loxodonta africana zone	1, 1A, 3, 6, 7, 7A, 8, 8A	Ileret Member, Koobi Fora Formation	*Elephas recki* stage 3–4 *Loxodonta africana* *Mesochoerus limnetes* (very progressive) *Metridiochoerus andrewsi* (progressive) *Hippopotamus* cf. *amphibius* *Ceratotherium simum* (very progressive)
Metridiochoerus andrewsi zone	6A, 8B, 10, 102, 103, 104, 105b	Upper member, Koobi Fora Formation	*Elephas recki* stage 3 *Mesochoerus limnetes* (progressive) *Metridiochoerus andrewsi* (typical) *Hippopotamus* sp. nov. (typical) *Ceratotherium simum* (progressive) *Tragelaphus* cf. *grandis*
Mesochoerus limnetes zone	105a, 130, 123	Lower member, Koobi Fora Formation	*Elephas recki* stage 2 *Notochoerus euilus* (progressive) *Mesochoerus limnetes* (typical) *Hippopotamus* sp. nov. (early) *Ceratotherium simum* (early) *Tragelaphus nakuae*
Notochoerus capensis zone	201, 202, 203	Kubi Algi beds	*Elephas ekorensis* *Notochoerus capensis* *Nyanzachoerus* sp. *Hippopotamus* sp. nov. (very early)

Vertebrate fossil zones of East Lake Rudolf.
From Maglio (1972): 382.

Figure II - 19


ILERET REGION
KOOBI FORA RIDGE N. EAST
KOOBI FORA RIDGE S. WEST
KUBI ALGI REGION
Galana Boi beds
Galana Boi beds
Guomdi Fm.
Chari tuff
3
1, 1a, 6, 6a,
7, 7a, 8, 8a
Loxodonta africana Zone
Metridiochoerus andrewsi Zone
6b, 8b, 10, 12
Koobi Fora Fm.
KBS Tuff
upper mb.
105b
upper mb.
101, 102, 103, 104
Mesochoerus limnetes Zone
lower mb.
105a, 130, 131
lower mb.
129
Suregei tuff complex
Notochoerus capensis Zone
Kubi Algi beds
201
202
203
(4.6 ± 0.1 m.y.)

Approximate correlation of lithostratigraphic units at East Rudolf and distribution of faunal zones. Major fossil collecting areas are indicated to the right of each section. From Maglio (1972): 383.

From the faunal evidence the total span of time represented at East Rudolf ranges from 4.5 million years to about 1.3 million years with the faunal sequence the oldest faunal zone, of *N. capensis*, correlates with the assemblages from the Mursi (Omo) and Kanapoi Formations. The *M. andrewsi* zone fauna compares well with faunas from Olduvai Bed I and lower Bed II, both younger than 1.85 million years. Correlates of the *Loxodonta africana* zone are not well established but appear to be older than Bed IV Olduvai suggesting that the inferred age of 1.3 million years is approximately correct.

EAST LAKE RUDOLF

Fossil Inventory

Found	Site	Number	Description	Published
1968	KF	KNM ER 403	R. mandible corpus	Leakey, Mungai, Walker, 1971
1968	KF	KNM ER 405	Maxilla edentulous	"
1968	I	KNM ER 404	R. mandible corpus	"
1968	I	KNM ER 417	Fragment parietal	"
1969	I	KNM ER 406	Cranium, edentulous	"
1969	I	KNM ER 407	Cranium, lacking face and maxilla	Leakey, 1971
1969	KF	KNM ER 164	Fragment parietal	"
1970	I	KNM ER 725	L. mandible corpus, edentulous	Leakey, Mungai, Walker, 1972
1970	I	KNM ER 726	L. mandible corpus, edentulous	"
1970	I	KNM ER 727	R. mandible corpus, edentulous	"
1970	I	KNM ER 728	R. mandible corpus, edentulous	"
1970	I	KNM ER 729	Mandible with dentition	"
1970	I	KNM ER 732	R. cranium, maxilla, frontal parietal	"
1970	KF	KNM ER 730	L. mandible corpus, M_1-M_3, symp to RP_4	Leakey, 1971
1970	I	KNM ER 731	L. fragment mandible corpus	"
1970	I	KNM ER 733	Cranial fragments, maxilla fragment, L. mandible	"
1970	KF	KNM ER 734	Fragment parietal	"
1970	KF	KNM ER 736	L. femur, shaft	Leakey, Mungai, Walker, 1972
1970	KF	KNM ER 738	L. femur, proximal end and shaft	"
1970	I	KNM ER 739	R. humerus, distal end and shaft	"
1970	I	KNM ER 740	L. humerus, fragment of distal end	"

ound	Site	Number	Description	Published
1970	I	KNM ER 741	L. tibia, proximal end and shaft	Leakey, Mungai, Walker, 1972
1970	KF	KNM ER 737	L. femoral shaft	Leakey, 1971
1971	I	KNM ER 164	Additional two vertebrae, hand bones	Day, Leakey, 1974
1971	I	KNM ER 803	Partial skeleton, postcrania, teeth	"
1971	I	KNM ER 999	L. femur lacking lateral condyle	"
1971	I	KNM ER 801	R. mandibular corpus M_2-M_3	Leakey, 1972
1971	I	KNM ER 802	Isolated adult teeth	"
1971	I	KNM ER 805	L. mandibular corpus	"
1971	KF	KNM ER 810	L. mandibular corpus -M_3	"
1971	KF	KNM ER 812	Immature L. mandibular corpus	"
1971	KF	KNM ER 814	Cranial fragments, frontal parietal	"
1971	I	KNM ER 815	L. femur without head	"
1971	KF	KNM ER 816	L. upper canine	"
1971	I	KNM ER 818	L. mandibular corpus P_4-M_3	"
1971	I	KNM ER 819	L. mandibular corpus	"
1971	I	KNM ER 993	R. femur	"
1971	KF	KNM ER 997	Proximal metatarsal	"
1971	KF	KNM ER 996	Lateral incisor	"
1971	I	KNM ER 1170	Skull fragments	"
1971	I	KNM ER 1171	Isolated juvenile teeth	"
1971	I	KNM ER 806	Isolated teeth A-F	"
1971	I	KNM ER 807	Fragment L. maxilla	"
1971	I	KNM ER 808	Isolated upper teeth A-G	"
1971	I	KNM ER 809	Fragments teeth	"
1971	KF	KNM ER 811	Fragment parietal	"
1971	KF	KNM ER 813	R. talus, fragment tibia	"

Found	Site	Number	Description	Published
1971	KF	KNM ER 817	L. mandibular corpus	Leakey, 1972
1971	I	KNM ER 820	Immature mandible	"
1971	I	KNM ER 992	Mandible and dentition excluding incisors	"
1972	Area 131	KNM ER 1483	L. mandible fragment, roots I_2-M_1	Leakey, Wood, 1974
1972	Area 130	KNM ER 1462	Crown of lower M_3	"
1972	Area 105	KNM ER 1501	R. mandibular body, roots I_2-M_3	"
1972		KNM ER 1502	R. mandibular body, M_1, roots M_2	"
1972		KNM ER 1507	Lower juvenile mandibular body, alveoli decid. canine	"
1972		KNM ER 1508	Crown and root R M_1 or M_2	"
1972	KF Karari Escarp.	KNM ER 1470	Partial cranium	Day, Leakey, Walke Wood, 1975
1972	"	KNM ER 1481	L. femur, proximal and distal end tibia/distal fibula	"
1972	"	KNM ER 1472	R. femur	"
1972	"	KNM ER 1475	Proximal end and shaft of femur	"
1973	Area 130	KNM ER 1800	Cranial fragments	Leakey, 1974
1973	Area 131	KNM ER 1801	L. mandible, P_4, M_1, M_3	"
1973	Area 131	KNM ER 1802	L. mandible P_4-M_2 and R. P_3-M_2	"
1973	Area 131	KNM ER 1803	R. mandible fragment	"
1973	Area 104	KNM ER 1804	R. maxilla [illegible]	"
1973	Area 130	KNM ER 1805	Cranium and [illegible]	"
1973	Area 130	KNM ER 1806	Mandible	"
1973	Area 103	KNM ER 1807	R. femur shaft	"
1973	Area 103	KNM ER 1808	Assoc. skeletal and cranial fragments	"
1973	Area 127	KNM ER 1809	R. femur shaft	"
1973	Area 123	KNM ER 1810	Prox. left tibia	"
1973	Area 123	KNM ER 1811	L. mandibular fragment	"

Found	Site	Number	Description	Published
1973	Area 123	KNM ER 1812	R. mandibular fragment, left I_1 and M_1	Leakey, 1974
1973	Area 123	KNM ER 1813	Cranium	"
1973	Area 127	KNM ER 1814	Maxillary fragments	"
1973	I	KNM ER 1815	R. talus	"
1973	6A	KNM ER 1816	Immature fragments of mandible	"
1973	I	KNM ER 1817	R. mandible	"
1973	6A	KNM ER 1818	Upper I^1	"
1973	3	KNM ER 1819	M_3	"
1973	Area 103	KNM ER 1820	L. mandible with M_1	"

EAST RUDOLF

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1970 Preliminary geological interpretation of a new hominid site in the Lake Rudolf Basin. Nature 226: 225-226.

Behrensmeyer, A. K., C. F. Vondra, G. D. Johnson, and B. E. Bowen
1971 Preliminary stratigraphical studies of the East Rudolf Basin, Kenya. Nature 231: 245-248.

Bowen, B. E. and C. F. Vondra
1973 Stratigraphical relationships of the Plio-Pleistocene deposits, East Rudolf, Kenya. Nature 242: 391-393.

The geological investigation of the area east of Lake Rudolf, Northern Kenya, was initiated in 1969 by A. K. Behrensmeyer and continued by a team from Iowa State University in 1970, 1971 and 1972 as part of the National Museums of Kenya expedition. This report summarizes the stratigraphical relationships established during the 1971 and 1972 seasons of the Plio-Pleistocene sediments and formalizes the stratigraphical nomenclature.

Brock, A. and G. Isaac
1974 Paleomagnetic stratigraphy and chronology of hominid-bearing sediments east of Lake Rudolf, Kenya. Nature 247: 344-348.

This article describes techniques, uses and some results of paleomagnetic studies. Polarity stratigraphy of samples taken in the area east of Lake Rudolf compare favorably with the K/Ar and faunal evidence.

Day, M. H. and R. E. F. Leakey
1973 New evidence of the genus Homo from East Rudolf, Kenya, I. AJPA 39: 341-354.

Three new fossil hominid specimens that were recovered in 1970 from Plio-Pleistocene sediments are described. They include the left side of the body and the symphyseal region of an adult mandibular fragment (KNM 731) and the shaft of a left femur (KNM ER 737). The specimens are described in anatomical detail, illustrated and selected measurements given. Specimens were attributed to the genus Homo sp. indet.

1974 New evidence of the genus Homo from East Rudolf, Kenya, III. AJPA 41: 367-379.

Announcement of a new fossil hominid partial skeleton (KNM ER 803). Post crania, teeth are described, including large left femur (KNM ER 999).

Day, M. H., R. E. F. Leakey, A. Walker and B. Wood
1975 New hominids from East Rudolf, Kenya, I. AJPA 42: 461-475.

Announcement of new hominid fossils (KNM ER 1470) consisting of an adult cranium and post cranial materials.

Fitch, F. and J. Miller
1970 Radiometric age determinations of Lake Rudolf artifact site. Nature 226: 226-228.

Fitch, F., J. Miller, I. C. Findlater, and R. Watkins
1974 Dating of rock successions containing fossil hominids at East Rudolf, Kenya. Nature 251: 213-214.

The main conclusion of the 1970-1973 dating program was discussed, although full publication of the results of these and other projects must await the completion of the field mapping. This dating work on the rocks from the East Rudolf Basin, completed in 1973, confirms the suggested age of 2.62 ± .26 million years reported for the KBS Tuff in 1970 and places it within a chronologically satisfactory sequence of dated tuffs.

Hurford, A.J.
1974 Fission track dating of a vitric tuff from East Rudolf, North Kenya. Nature 249: 236-237.

The apparent age obtained by fission track dating correlates with and supports previous dates obtained by K.Ar and 40Argon/39Argon studies. Thus it is shown that fission track dating is practical when applied to Plio-Pleistocene vitric tuff.

Isaac, G., R. Leakey and A. Behrensmeyer
1971 Archaeological traces of early hominid activities east of Lake Rudolf, Kenya. Science 173: 1129-1134.

Stone artifacts discovered within beds of Lower Pleistocene age occur together with small quantities of broken bones. This locality was said to perhaps be the oldest known human occupation site.

Kay, R.
1973 Humerus of robust *Australopithecus*. Science 182: 396.

Gives a functional interpretation of the morphological differences seen in the robust *Australopithecus* humerus KNM ER 739 from Lake Rudolf. By discriminant analysis it was concluded that *A. robustus* used his forelimb in some form of locomotion.

Leakey, M.
1970 Early artifacts from the Koobi Fora area. Nature 226: 228-230.

Leakey, R. E. F.
1970 In search of man's past at Lake Rudolf. National Geographic 137: 712-732.

1971a Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya. Nature 231: 241-245.

Report describes the finding of the 1970 Rudolf expedition which recovered sixteen new specimens of hominids. Both cranial and post cranial remains are described and from the author's point of view the material adds support that both *Australopithecus* and *Homo* lived contemporaneously during the LowerPleistocene.

1971b Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya. Nature 231: 241-244.

The author discusses the results of the 1970 ecpedition and gives description of specimen. It is stressed that most of the specimen can be assigned to the genus *Australopithecus* but they are not assigned to species. Evidence indicates australopithecine occupation of 1 million year duration, with a wide range of variability. This occurrence of Homo at East Rudolf is represented by three specimens, KNM ER 730, 731 and 737. No evidence is seen to indicate a relationship between *Homo* and *Australopithecus* in spite of their existing in the same time and habitat.

1972a Man and sub-men on Lake Rudolf. New Scientist, November 16, 1972, 385-387.

1972b Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya. Nature 237: 264-269.

A preliminary report of a collection of Lower Pleistocene hominids recovered from the East Rudolf area during the 1970 expedition was made and brought the total number of hominid specimens from East Rudolf to 23, including both cranial and post cranial elements. No attempt was made to assign specific taxonomic nomenclature to this material. In 1971 more hominid specimens were recovered from East Rudolf bringing the total to over 45. The exact location of each hominid find is marked in the field by an embedded concrete post; geological investigations have located the specimens to stratigraphical sections. Lists specimens attributed to *Australopithecus* and *Homo*.

1973a Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya, 1972. Nature 242: 170-173.

Thirty-eight fossil hominids were collected during the 1972 season at East Rudolf, and now the total known from this locality is 87. Several specimens, including some attributable to *Homo*, were recovered from deposits that are now below the KBS Tuff dated at 2.61 million years. This report summarizes the results of the continuation of work carried out during 1972 at East Rudolf. Photographs of KNM ER 1477, 1501, 1502, 1502, 1504, 1505 and 1507 are included.

1973b Evidence for an advanced Plio-Pleistocene hominid from East Rudolf, Kenya. Nature 242: 447-450.

Four specimens collected during 1972 are provisionally attributed to the genus *Homo*. One, a cranium KNM ER 1470, is probably 2.9 million years old. Preliminary descriptions are presented of the four specimens collected from East Rudolf during 1972: KNM ER 1470, 1472, 1475 and 1481. A map showing site of discovery of fossil hominids is given and includes a stratigraphical succession of sediments with the vertical relationship to the hominid specimens. Photographs of the cranium KNM ER 1470 and the left femur KNM ER 1481 are included.

1974 Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya, 1973. Nature 248: 653-656.

Reports of the 1973 field season at East Rudolf, Kenya concluding its sixth year of operations. Eighty-seven specimens of fossil hominid were collected from the area during 1968-1973; a further 20 specimens were recovered between June and September 1973 from the upper, lower, and Ileret members of the Koobi Fora Formation. Exploration to the south of Koobi Fora was begun in 1972 and continued in 1973. No hominids have yet been found in the limited exposures of the Kubi Alga Formation. A notice of two specimens KNM ER 1510 and 1590 is included in this report. The 1973 hominids are not here attributed to genera. Previous attributions for the East Rudolf hominid collection remain satisfactory. Photographs of KNM ER 1802, 1813 are included.

Leakey, R. E. F., et. al.

1970 Fauna and artifacts from a new Plio-Pleistocene locality near Lake Rudolf in Kenya. Nature 226: 223-224.

This report gives some of the results of the two 3-month expeditions (1968-1969) into the Lake Rudolf area of Kenya. This report is divided into four parts. Fauna and Artifacts from a New Plio-Pleistocene Locality Near Lake Rudolf in Kenya by R. E. F. Leakey; Preliminary Geological Interpretation of a New Hominid Site in the Lake Rudolf Basin by A. K. Behrensmeyer; Radioisotopic Age Determinations of Lake Rudolf Artifact Site by F. J. Fitch and J. A. Miller; Early Artifacts from the Koobi Fora Area by M. Leakey. "Five hominid specimens, including two well preserved crania, early artifacts and a rich collection of vertebrates have been found and recovered from Plio-Pleistocene deposits near Lake Rudolf. Some of the artifacts were located 'in sight' in a horizon that has since been reliably dated with a new isotopic technique and 2.61 ± .26 million years. They constitute the oldest known 'insite' dated unequivocal artifacts."

Leakey, R. E. F. and G. Isaac

1972 Hominid fossils from the area east of Lake Rudolf, Kenya: photographs and a commentary on context. IN Perspectives on Human Evolution, S. Washburn and P. Dolkinow, eds., 129-130.

Summarizes the hominid fossils discovered up to 1970. Reviews the evidence of stratigraphy, dating and archaeology and states a plan for future work at East Rudolf.

Leakey, R. E. F., J. M. Mungai, and A. Walker

1971 New australopithecines from East Rudolf, Kenya. AJPA 35: 175-186.

Five specimens discovered during 1968-1969 field surveys are described. Specimens KNM ER 404, 406 and 417 were recovered from localities below the KBS Tuff and specimens KNM ER 403, and 405 were recovered from localities above the tuff.

1972 New australopithecines from East Rudolf, Kenya (II). AJPA 36: 235-252.

Eleven specimens of fossil hominids are described consisting of cranial and post cranial elements. All were assigned to the genus Australopithecus: KNM ER 725, 726, 727, 728, 729, 732, 736, 738, 739, 740 and 741.

Leakey, R. E. F. and A. Walker

1973 New australopithecines from East Rudolf, Kenya (III). AJPA 39: 205-222.

·A further ten australopithecine specimens from the Plio-Pleistocene deposits of East Rudolf, Kenya are described. These include a fragmentary skull, several mandibles and two pieces of femur. These specimens are numbered KNM ER 733, 801, 802, 805A and B, 810, 812, 814, 815, 818, 819, 993 and 1171.

Leakey, R. E. F. and B. Wood

1973 New evidence of the genus Homo from East Rudolf, Kenya, II. AJPA 39: 355-368.

Eight specimens attributed to Homo from East Rudolf, Kenya are described. They include two well-preserved mandibles and a smaller mandibular fragment, an associated talus and tibial fragments and a collection of isolated teeth. Measurements of the mandibles and teeth KNM ER 992 are listed and photographs of mandibles KNM ER 992 and KNM ER 820 and the talus KNM ER 813, the maxilla KNM ER 807 and the mandible KNM ER 817 are included.

Maglio, V. J.

1971 Vertebrate faunas from the Kubi Algi, Koobi Fora and Ileret Areas, East Rudolf, Kenya. Nature 231: 248-249.

The 600 fossil vertebrates are shown to be representative of two faunal units. One Pliocene is poorly known, the other is Pleistocene. Some of the specimens are briefly described and discussed as are their relationships to specimens from other sites.

1972 Vertebrate faunas and chronology of hominid-bearing sediments east of Lake Rudolf, Kenya. Nature 239: 379-385.

The vertebrate faunas which have been collected from east of Lake Rudolf include hominid remains and the earliest dated stone artifacts known. It is now possible to recognize faunal units and to establish tentative chronology for observed faunal units. It is suggested here that the faunal sequence at East Rudolf may extend from 4.5 million years to about 1.3 million years with a significant break between about 4.0 and 2.6 million years in correlation of faunal zones.

McHenry, H. M.

1973 Early hominid humerus from East Rudolf, Kenya. Science 180: 739-741.

Fossil hominid humerus KNM ER 739, discovered in 1970 by the expedition to East Rudolf, Kenya, is examined in comparison with a large series of extant hominoids. This comparison, as well as multiple discriminant analysis, shows the uniqueness of the fossil among the hominoids.

Robinson, J. T.
1972 The bearing of East Rudolf fossils on early hominid systematics. Nature 240: 239-240.

> The author states, "Here I suggest that, on the contrary, his (Leakey's) interpretations of the East Rudolf material and mine of the South African finds are in remarkably close agreement; the difference between them is more apparent than real and stems from nomenclature rather than biological considerations."

Vondra, C. F., G. Johnson, B. E. Bowen and A. K. Behrensmeyer
1971 Preliminary stratigraphic studies of the East Rudolf Basin, Kenya. Nature 231: 245-248.

> This article outlines the general stratigraphy and depositional environment of the sedimentary units studied in the East Rudolf area.

NORTH LAKE RUDOLF

LOWER OMO BASIN

GEOCHRONOLOGY

Southward from the Ethiopian highlands the Omo River empties into the northern end of Lake Rudolf producing an extensive delta. Beginning during the 1930's, these exposures of Plio-Pleistocene age have been extensively explored by the late C. Arambourg, and joined more recently by Yves Coppens, Jan de Heinzelin and F. Clark Howell. From radiometric determinations on lavas and interbedded tuffs, the Omo succession spans a range of time from more than 4 million years to less than 2 million years.

The oldest sediments exposed in the Lower Omo Basin are those of the Mursi Formation which outcrop at the Yellow Sands locality near the southwestern edge of the Nkalabong highlands. This formation comprises three sedimentary members (I-III) composed primarily of clays, salts and sands with an aggregate thickness of over 140 meters and a terminal basalt member (IV). The sediments in members I and II are primarily deltaic with some evidence of fluvio-littoral conditions in the upper deposits. Radiometric determinations of the basalt of member IV yield a mean age of 4.2 million years. The fossil fauna, especially the Suidae and Proboscidea, closely resemble those of Kanapoi.

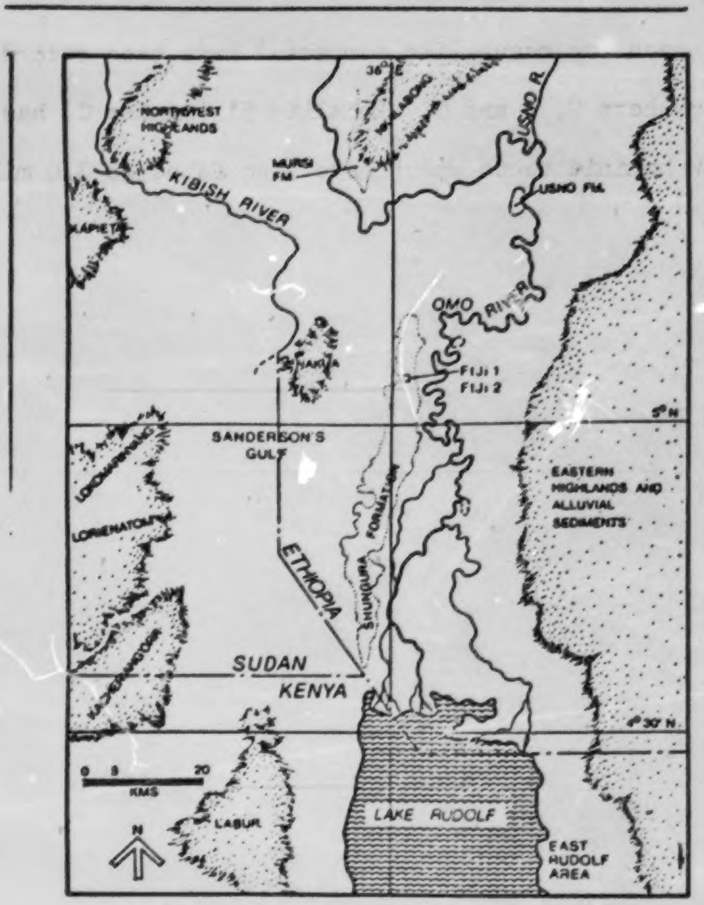
The Nkalabong Formation unconformably overlies basalt member IV of the Mursi Formation. Its total thickness is nearly 90 meters and it has been lithologically divided into three members. The succession represents fluviatile deposits followed by wind deposited volcanic ash after which a series of littoral and tuff deposits were accumulated. Lacustrine deposits are common in the uppermost member of the Formation. No fossiliferous localities have been discovered but two K/Ar determinations on feldspars from the Lapilli tuff (top of member II) have yielded an age of 3.95 million years.

In the northeastern corner of the basin outcrops of sediments and lavas of the Usno Formation have a total aggregate thickness of about 200 meters. The sequence has been subdivided into nine members (A-I) which appear to represent fluviatile deposits, the result of floodplain and swamp situations. Two localities, designated White Sands and Brown Sands, have yielded some 20 hominid teeth among an extensive vertebrate fauna. Radiometric determinstions on the basal lava sequence (B) yielded an age of 3.3 million years. From member G, the triple tuff sequence, an age of 2.6 million years was also determined. This age is equivalent to member C of the more southern Shungura Formation exposures.

The Shungura Formation (= Omo Beds) are the principal exposures between the Nakua volcanic hills and the lower reaches of the Omo River. The overall thickness of this formation is about 600 meters and represents a series of fluvial deltaic and lacustrine sands, silts and clays with intercollated tuffs. Ten prominent tuffs (designated A through J upwards) form marker horizons within the succession. A series of radiometric dates have been determined which span from 3.75 million years (member B) to 1.84 million years (member I). The stratigraphy of the sedimentary deposits have been investigated by Brown and Lajoie (1970) and consist of a basal member underlying a cyclic lithologic sequence of silts overlain by coarse to fine sands and silts and clays of members A through J, the result of rhythmic fluviatile deposition. Member I is the uppermost deposit in the series and is comprised of a fine pumice gravel. The Kalam West exposures, south of the Nakua volcanic hills, have recently been tied into the main Shungura succession and represent deposits younger than member J. Three additional members K, L, and M are recognized above Tuff J and its overlying sediments. Tuff L has a radiometric age of 1.3 million years. After deposition the Shungura Formation, like the Usno Formation, was extensively faulted and both formations are unconformably overlain by upper Pleistocene/Holocene Kibish Formation. Comparable deposits overlie the Koobi Fora succession in the East Rudolf.

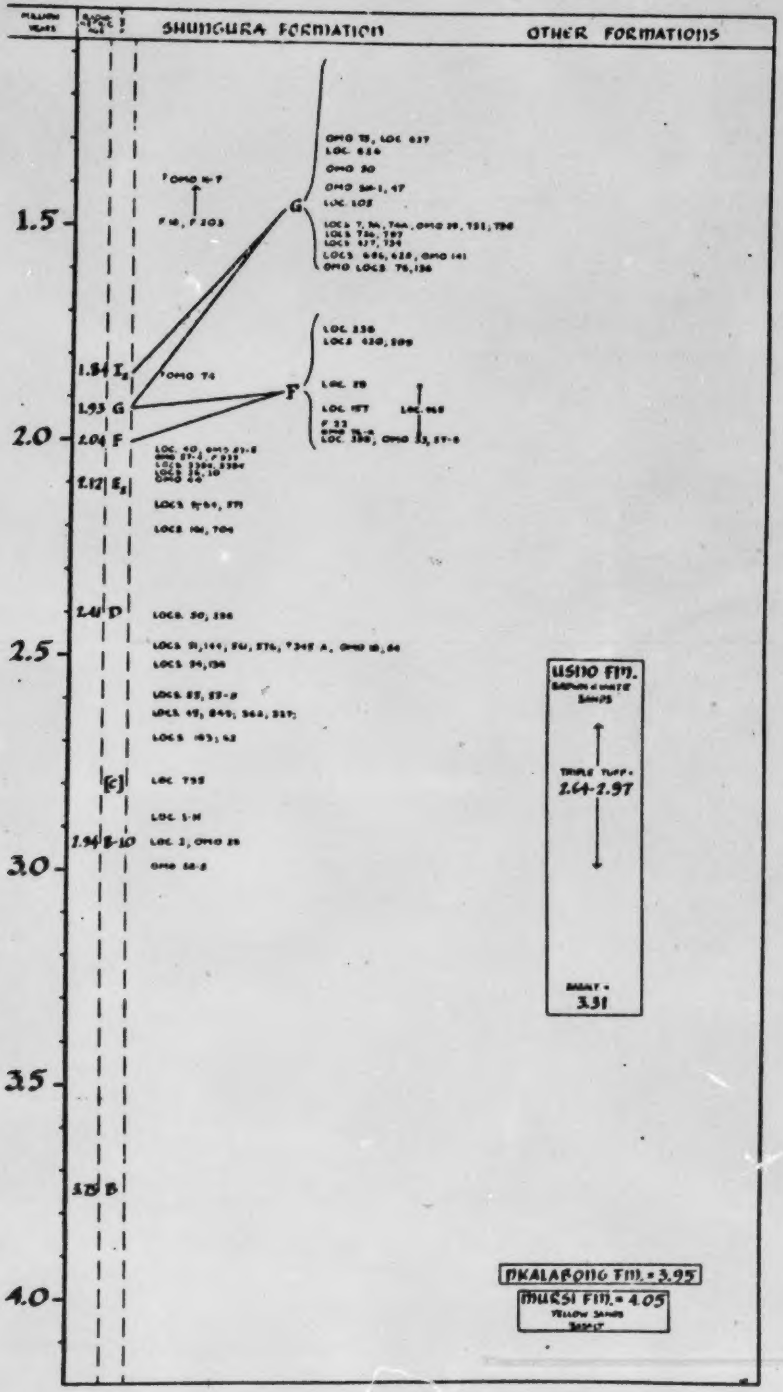
Localities yielding artifacts are not common in the main Omo deposits and absent from the Mursi and Usno succession. One locality (within member E of the Shungura Formation) has yielded a few artifacts and fragmentary bone. Other sparse occurrences (no occupation surfaces) have been recorded in sediments and tuffs of members G, D and C. Locality 51 (member C) has yielded artifacts plus a few hominid teeth which have been dated at 3.0 million years.

Figure II - 20


NORTHWEST HIGHLANDS
36° E
USNO R.
MURSI FM
USNO FM
KIBISH RIVER
KAPIETA
OMO RIVER
NAKUA
FIJI 1
FIJI 2
5° N
SANDERSON'S GULF
EASTERN HIGHLANDS AND ALLUVIAL SEDIMENTS
LORIENATOM
SHUNGURA FORMATION
ETHIOPIA
SUDAN
KENYA
4° 30' N
0 5 20
KMS
LAKE RUDOLF
LABUR
N
EAST RUDOLF AREA

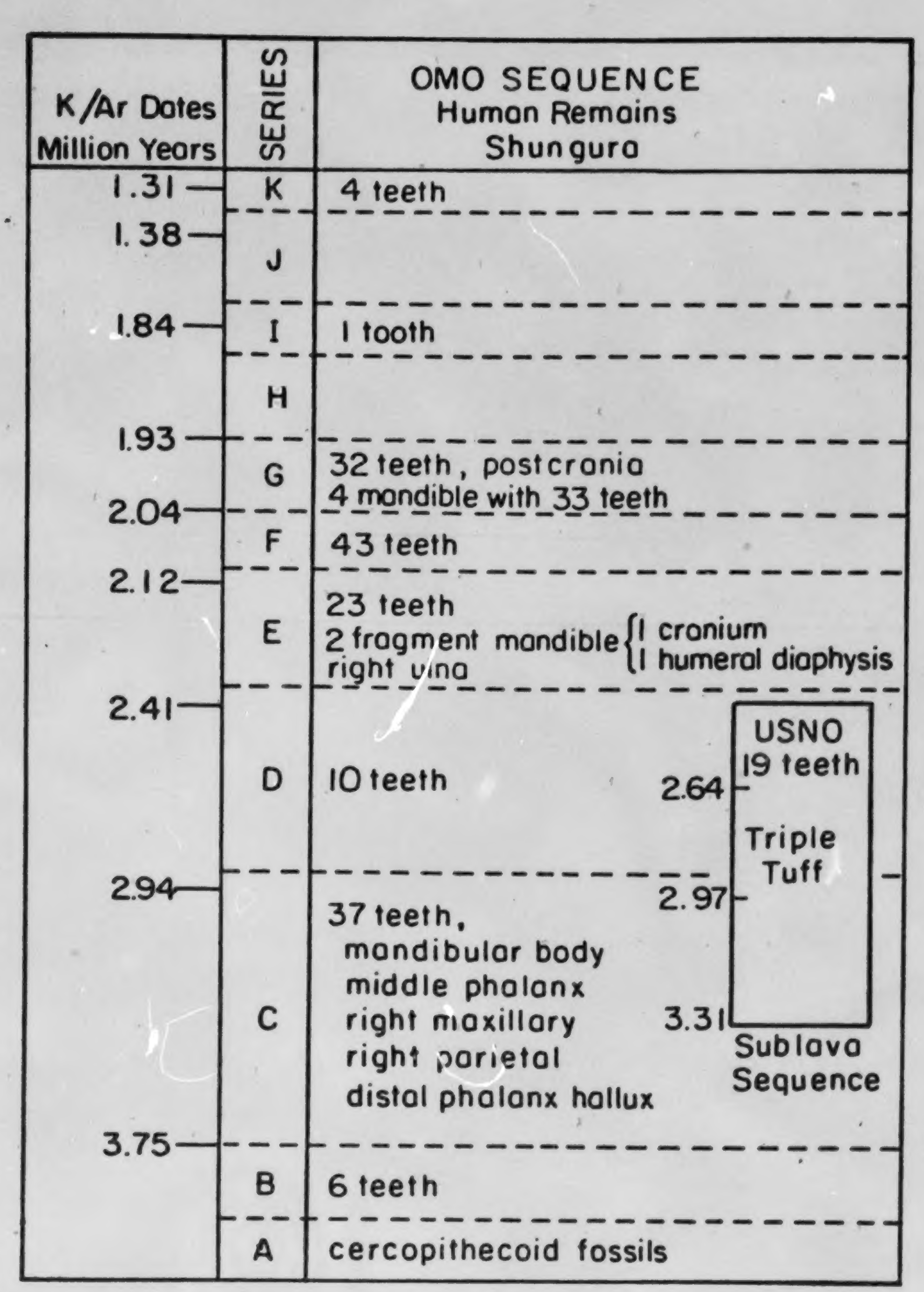
Generalized map of the lower Omo Basin, Ethiopia, showing the locations of the hominid bearing exposures.
(From Merrick et. al. (1973):572)

Figure II - 21



Stratigraphic relationship of hominid bearing localities of the Shungura and other formations of the Omo Succession, Ethiopia.
(From Howell and Coppens (1974):4)

Figure II - 22


USNO
19 teeth
2.64
Triple Tuff
2.97
3.31
Sublava Sequence

K/Ar Dates Million Years	SERIES	OMO SEQUENCE Human Remains Shungura
1.31	K	4 teeth
1.38	J	
1.84	I	1 tooth
	H	
1.93	G	32 teeth, postcrania 4 mandible with 33 teeth
2.04	F	43 teeth
2.12	E	23 teeth 2 fragment mandible {1 cranium 1 humeral diaphysis right ulna
2.41	D	10 teeth
2.94	C	37 teeth, mandibular body middle phalanx right maxillary right parietal distal phalanx hallux
3.75	B	6 teeth
	A	cercopithecoid fossils

OMO

Fossil Inventory
(AJPA (1974) 40(1))

Locality	Number	Description
Usno Fm. Brown Sands	B8-27	right I^1
	B8-23a	left P^4
	B8-14a	left P^4
	B8-14b	left P^4
	B8-4q	left P^4
	B8-23b	left m^1
	B7-39a	left P^3
	B7-39b	left P^4
	B7-36c	inc. m^1
	B-20	inc. dm^2
	B-28	inc. dm_2
White Sands	W-23	left P_4
	W-508	right m_1
	W-749	right m^2
	W-752	right m_1
	W-578	inc. left m_1
	W-750	frag. P^3
	W-751	inc. P_4
	W-753	right dm^2
Shungura Fm. Member A Loc 2	2-79	inc. $m_{2/3}$
	2-89	left m_3
Loc 1 North	1-292	frag. $\underline{P}$.
	1-294	right m_3

Locality	Number	Description
Shungura Fm.		
Member A		
Loc Omo 28	28-19 (1967)	frag. right m_3
Loc Omo 28-S	28-30 (1968)	right m_3
Member C		
Loc Omo 18	18-18 (1967)	corpus mandible
	18-31 (1968)	left P^3
	18-32 (1968)	right m^1
	18-33 (1968)	left P_3
	18-34 (1968)	left m_1 or 2
	18-35 (1968)	frag. $\underline{M}$
	18-36 (1968)	left I^1
	18-37 (1968)	right I^2
	18-38 (1968)	right I^2
	18-39 (1968)	right I^1
	18-40 (1968)	left I_1
	18-1799 (1970)	left m^1
	18-1848 (1970)	left middle phalanx, hand
Loc 45	45-2	right m_1
Loc 51	51-1	left m_1
	51-2	left m^1
	51-3	left m^2
	51-4	left m^1
	51-5	right I^1
	51-6	frag. right m^2
	51-7	inc. right $\overline{M}$
	51-79	right P_4
	51-80	right P_4

Locality	Number	Description
Shungura Fm. Member C		
Loc 54	54-20	inc. r. dm^2
Loc 55	55-33	right maxilla, roots $I^1 \longrightarrow P^3$, P^4 crown
	55-34	frag. M
	55-57	left I^2
Loc 852	852-15	right I^1
Loc 849	849-1	frag. right m_3
Loc 62	62-17	right m_2
Loc Omo 84	84-100 (1970)	right m_3
Loc 136	136-9	frag. m_3
Loc 144	144-23	left dm^2
	144-24	inc. right dm_2
Loc 183	183-11	frag. $\underline{M}$
Loc 327	327-16	I^2
Loc 345(A)	345(A)-11	subadult right parietal fragment
Loc 362	362-14	m_1
Loc 561	561-1	frag. left I^2
Loc 576	576-27	right dm_2
	576-18	right(?) distal phalanx hallux
Loc 795	795-1	right m_3
Member D		
Loc 9	9-11	inc. right m_3
	9-12	left m^3
	9-92	inc. left $m^{1/2}$
Loc 50	50-2	left m^3
Loc 64	64-2	left dm_2
	64-23	inc. dm_1 (?)
Loc 161	161-34i	frag. C (?)
Loc 296	296-1	right m_3

Locality	Number	Description
Shungura Fm. Member D		
Loc 571	571-2	left I^1
Loc 704	704-2	left dm_1
Member E		
Loc 10	10-21	inc. right m_3
Loc 26	26-1g	right m_2
	26-59	inc. left $m^{2/3}$
Loc 40	40-19	right ulna
Loc Omo 44	44-2466 (1970)	frag. mandible with roots of dentition
	44-1410 (1970)	right P^3
Loc Omo 57-4	57-41 (1968)	right hemi mandible, frag. right P_4
	57-42 (1968)	inc. left m_1
	57-4.147 (1972)	frag. left m^3
	57-4.148 (1972)	frag. right P^3
Loc Omo 57-5	57-5.123 (1972)	frag. P.
	57-5.197 (1972)	frag. M.
	57-5.370 (1972)	frag. M.
	57-5.371 (1972)	frag. M.
	57-5.372 (1972)	frag. M.
Loc Omo 57-6	57-6.244 (1972)	inc. right m^2
Loc 338X	338X-32	frag. left dm^2
	338X-33	inc. P^3
	338X-34	left m^2
	338X-35	right P^4
	338X-39	left m_3
	338X-40	left P_4
	338X-41	right C
	338X-42	frag. M

Locality	Number	Description
Shungura Fm. Member E Loc 338Y	338Y-6	juvenile cranium, occipital with foramen magnum, left/right parietals
	338Y-9	juvenile humeral shaft
	338Y-89	frag. P^4
Loc P.933	P.933-1	left m^1
Member F Loc (Kalam) F.22	F.22-1a	right m_2
	F.22-1b	right m_3
Loc 28	28-28x	frag. left P_3
	28-30	right m_3
	28-31	right m_2
	28-58	right m^2
	28-125	right $\bar{C}$
	28-126	$\underline{P}$
Loc Omo 33	33-9 (1969)	right m_3
	33-10 (1969)	left m_2
	33-62 (1970)	right m^3
	33-63 (1970)	right $m^{1/2}$
	33-64 (1970)	frag. $\underline{m}$
	33-65 (1970)	left m_3
	33-506 (1971)	right P^3
	33-507 (1971)	left m^3
	33-508 (1971)	right P_4
	33-509 (1971)	left $\underline{m}$
Loc Omo 76	76-13 (1969)	frag. left m_3
	76-37 (1972)	frag. left m_3
	76-38 (1972)	frag. M/P
Loc Omo 76r	76r-11 (1969)	frag. right m_2

Locality	Number	Description
Shungura Fm. Member F		
Loc Omo 76r	76r-12 (1969)	frag. left $m_{1/2}$
Loc 157	157-35	left m_2
Loc 209	209-17	frag. $m_{1/2}$
	209-18	frag. $\underline{m}$
	209-30	frag. m
	209-31	frag. m
Loc 238	238-35	right m^2
Loc 398	398-14	frag. right m_1
	398-120	right P_3
	398-264	frag. right m_1
	398-265	frag. I
	398-266	frag. right m_3
	398-573	left m^3
	398-630	right m_3
	398-847	frag. right m_3
	398-1223	right P_4
	398-1215	frag. m
Loc 420	420-15	left P_4
Loc 465	465-111	frag. left P_4
	465-112	frag. left P_4
	465-113	frag. P
Member G		
Loc Omo SH-1	SH-1-17 (1969)	left m^1
Loc 7	7-279	left m_2
Loc 7A	7A-125	mandible with teeth excluding three incisors
Loc Omo 29	29-43 (1968)	right P_3

Locality	Number	Description
Shungura Fm. Member G		
Loc Omo 47	47-45 (1968)	left m_1
	47-46 (1968)	right m_2
	47-47 (1968)	frag. right m_3
	47-20 (1969)	frag. $\underline{m}$
Loc Omo 50	50-44 (1968)	right I^2
Loc 74A	74A-21	right hemimandible with $\bar{C}$ and P_4
Loc Omo 75	75-14a, b (1969)	associated upper and lower dentition with portion of right mandibular body left P_3, m_1-m_3; $P^4 \rightarrow m^2$ right $P_3 \rightarrow m_2$; $P^4 \rightarrow m^3$
Loc Omo 75i	75i-1255 (1970)	right P_3
Loc Omo 75-s	75-s-15 (1969)	left m_1
	75-s-16 (1969)	right m_3
	75-s-875 (1970)	right I_2 or $\bar{C}$
	75-s-1317 (1970)	proximal radius
Loc 105	105-7	lumbar vertebra
Loc Omo 136	136-72-1	left m_3
	136-72-2	inc. left m_3
	136-72-3	frag. right $\underline{m}$
Loc Omo 141	141-72-1	frag. left m^3 (?)
	141-72-2	frag. left $m^{1/2}$
Loc 427	427-7	partial right hemimandible erupting P_3-P_4, roots of dm_2 and m_1, complete m_2
Loc 626	626-45	left I^1
Loc 628	628-1	left P^4
	628-2	inc. left m_3
	628-3	left m_3

Locality	Number	Description
Shungura Fm. Member G		
Loc 628	628-4	left P_4
	628-5	left P^4
	628-6	right I^1
	628-7	frag. m
	628-8	inc. $\underline{m}$
	628-9	left m_2
	628-10	left m_1
	628-224	inc. left P^3
Loc 686	686-3	left I^2
Loc 726	726-11	inc. P^3
Loc 754	754-8	part femoral diaphysis
Loc 797	797-1	frag. left P_4
Loc Omo 74	(Tuffs 12-14)	right P_4
Member L		
Loc (Kalam) F.203-1	F.203	right m_3
Loc Omo K-7	K-7-19 (1969)	left m_2
Loc (Kalam) F.18-3	F.18	left I^2

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LAKE BARINGO

Fossiliferous sediments from three localities in the Baringo Basin, Northern Rift Valley of Kenya, have produced faunal remains dating from about 1.0 million years to 12.0 million years.

Pliocene/Pleistocene sediments to the southwest of the Lake Baringo area and east of the Kamasia Hills were first recorded by Gregory and later described as the Kamasia sediments. These sediments actually represent two sedimentary sequences separated by a period of lava outpouring. The lower sequence has been named the Chemeron Beds, the upper sediments, which rest unconformably on the lower ones, has been named the Kapthurin Beds.

The Chemeron Beds are extensively faulted, have an aggregate thickness of some 250 meters, and are divided into five principal units. These units consist of (1) the Basal Beds, which have yielded a fossiliferous mammalian assemblage and are composed of fluviatile gravels and coarse angulated sands, (2) the Lower Fish Beds, represented by fluviolocustrine silts and superimposed locustrine silts and shelly limestones separated from (4) the Upper Fish Beds by Layer (3), the Lower Tuffs. Layer (5) is a series of waterlaid, stratified tuffs.

The sedimentary sequences are overlain by fine-grained lavas yielding K/Ar ages between 1.5-2.0 million years. Faunal analysis of several localities within the Basal Beds, however, show similarities to assemblages from Kanapoi and the Mursi Formation of the lower Omo Basin indicating much older ages nearer to 4.0 million years.

The only remains of Hominidae known from the Chemeron Beds consist of an isolated temporal bone from locality JM 85 in the Upper Fish Beds. The bone includes the mandibular fossa, the tympanic and external auditory meatus, part of the mastoid, root of the zygoma and most of the petrosal. The bone has been described by Tobias (1967), who suggested that most of the features of the temporal resemble those of known species of australopithecine.

Lying below outcrops of the Chemeron and underlying Kaporaina Basalt is a recently described series of deposits named the Lukeino Formation and described by Pickford (1975). Mapped during 1973 as part of the investigations of Bedford College, London, these exposures extend our knowledge of sediments and associated vertebrate assemblages back to 6.5 million years.

The Lukeino Formation is composed of about 130 meters of primary and reworked volcanic rock and basin deposited sediments. It is exposed over an area of 450 Km^2, but the outcrop is not continuous. Lying below these deposits is the Kabarnet Trachyte Formation which has yielded a K/Ar date of 6.7-7.0 million years. The sedimentary group is composed of four recognized members A-D (earliest to latest) with three sills intruded into the members, two of which were embedded before the deposition of Member D. The third sill (the Cheseton Sill) is not represented in the type section shown in Figure II - 23.

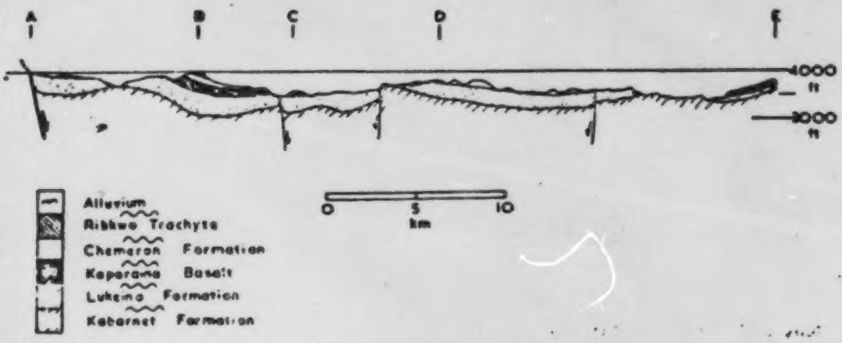
Relative uplift after the deposition of Member D resulted in erosion of the formation to the basal member. The eroding exposures were then capped by basalts of the Kaparaina Formation, radiometric determinations of which have given a minimum age for the Formation of 5.4 million years.

A list of fauna collected from the Lukeino Formation from forty-seven localities is provided. Most of the fossils were recovered from Members A and B. Hippopotamidae are abundant while the bovids, suids and giraffids are scarce. Paleoenvironmental reconstruction suggests prevalent lacustrine conditions during deposition. Fossil flora is also common in the form of leaves, grass, ferns and diatoms.

A single lower molar tooth represents the only hominid specimen to be recovered from these deposits to date. Although a surface find, the color of the tooth relates it to a fossiliferous horizon which lies in the middle of Member A at Locality 2/219 at Cheptoit. KNM LU335 is a left lower, probably unerupted, molar similar in general dimensions to the M_2 of the chimpanzee. In morphology it is similar to the robust forms of Australopithecus. The tooth is similar to the general hominid condition by having two equally divided occlusal basins indicating equal sized protocone and hypocone in the upper molar (as is the condition of the upper molar from the Ngorora

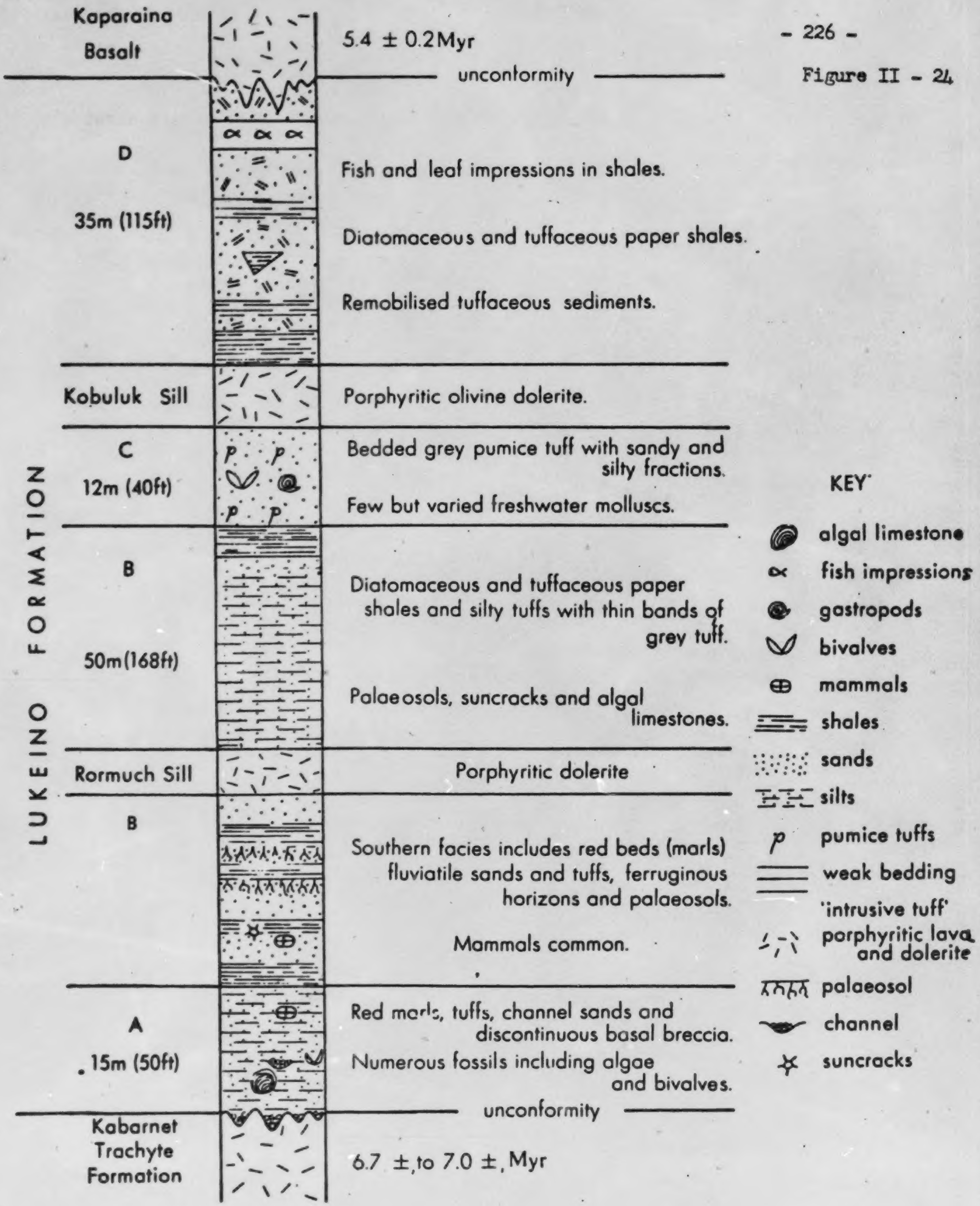
Formation). It is quite different from the Dryopithecine Pattern which shows a relatively smaller trigonid basin on the crown surface.

Figure II - 23


A
B
C
D
E
4000 ft
2000 ft
0
5
10
km
Alluvium
Ribkwo Trachyte
Chemeron Formation
Kaperama Basalt
Lukeino Formation
Kabarnet Formation

North-south section through the Lukeino Formation and overlying sediments. From Pickford, Nature 256 (1975): 281.

Figure II - 24


Kaparaina Basalt
5.4 ± 0.2Myr
unconformity
D
35m (115ft)
Fish and leaf impressions in shales.
Diatomaceous and tuffaceous paper shales.
Remobilised tuffaceous sediments.
Kobuluk Sill
Porphyritic olivine dolerite.
C
12m (40ft)
Bedded grey pumice tuff with sandy and silty fractions.
Few but varied freshwater molluscs.
LUKEINO FORMATION
B
50m(168ft)
Diatomaceous and tuffaceous paper shales and silty tuffs with thin bands of grey tuff.
Palaeosols, suncracks and algal limestones.
Rormuch Sill
Porphyritic dolerite
B
Southern facies includes red beds (marls) fluviatile sands and tuffs, ferruginous horizons and palaeosols.
Mammals common.
A
15m (50ft)
Red marls, tuffs, channel sands and discontinuous basal breccia.
Numerous fossils including algae and bivalves.
unconformity
Kabarnet Trachyte Formation
6.7 ±,to 7.0 ±,Myr
KEY
algal limestone
fish impressions
gastropods
bivalves
mammals
shales
sands
silts
pumice tuffs
weak bedding
'intrusive tuff'
porphyritic lava and dolerite
palaeosol
channel
suncracks

Type section of the Lukeino Formation at Kobuluk.
From Pickford, Nature 256 (1975): 280.

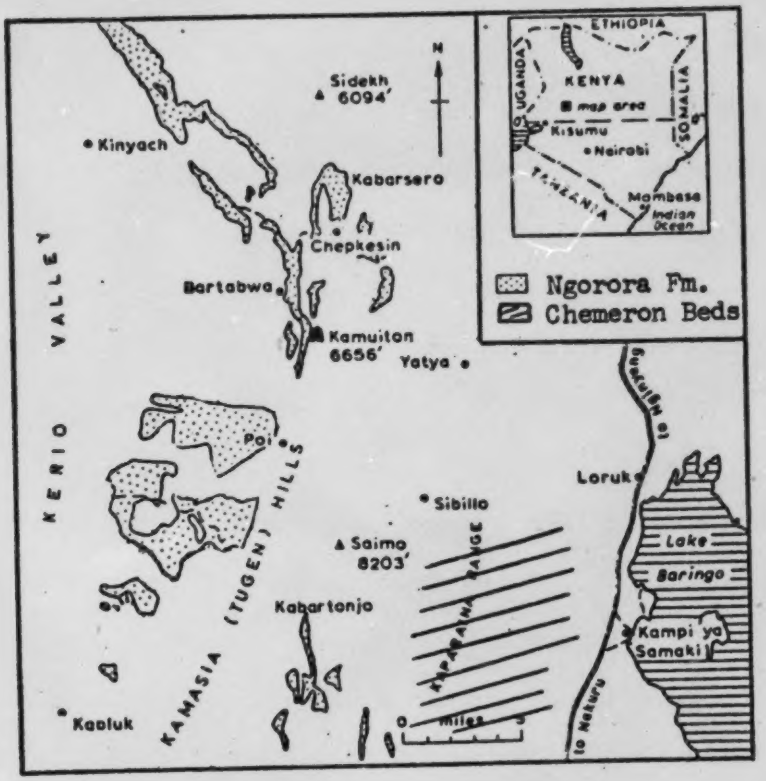
Older sedimentary outcrops which have yielded fossiliferous localities have been described by Bishop and Chapman (1970) on the western escarpment of the Kamasia Hills, twenty miles northwest of Lake Baringo. Investigated during 1968 and 1969, these fossiliferous sediments are underlain and overlain by lava flows yielding dates for the sediments between 9.0 and 12.0 million years. The sedimentary layers have been described as the Ngorora Formation and consist of lithologically variable waterlaid deposits some 360 meters in thickness. Five lithological subdivisions have been described labeled A-E. The single fossil hominid discovered was described by L. S. B. Leakey and consisted of an upper molar crown. Anterior and posterior wear facets are present suggesting that the tooth was an upper second molar. The crown was described as being very low relative to overall size and could be attributed to the genur *Australopithecus*.

To the east of Lake Baringo, additional sedimentary series were discovered by J. Carney in 1970. These sediments are contained in an embayment along the foot of the Aruru escarpment in the western part of the Chemoigut sedimentary basin. The basin itself was the result of upper Pliocene/Pleistocene volcanics which formed barriers damming the drainage from the eroded plateau region above the escarpment.

The fossiliferous sediments near Chesowanja have produced a series of fauna and flora species yielding data of the environment of perhaps 1.1 to 1.2 million years. Seven of the fourteen identified mammalian genera have modern counterparts in Africa, and the total assemblage has elements in common with that from Olduvai Bed II and Peninj in Tanzania.

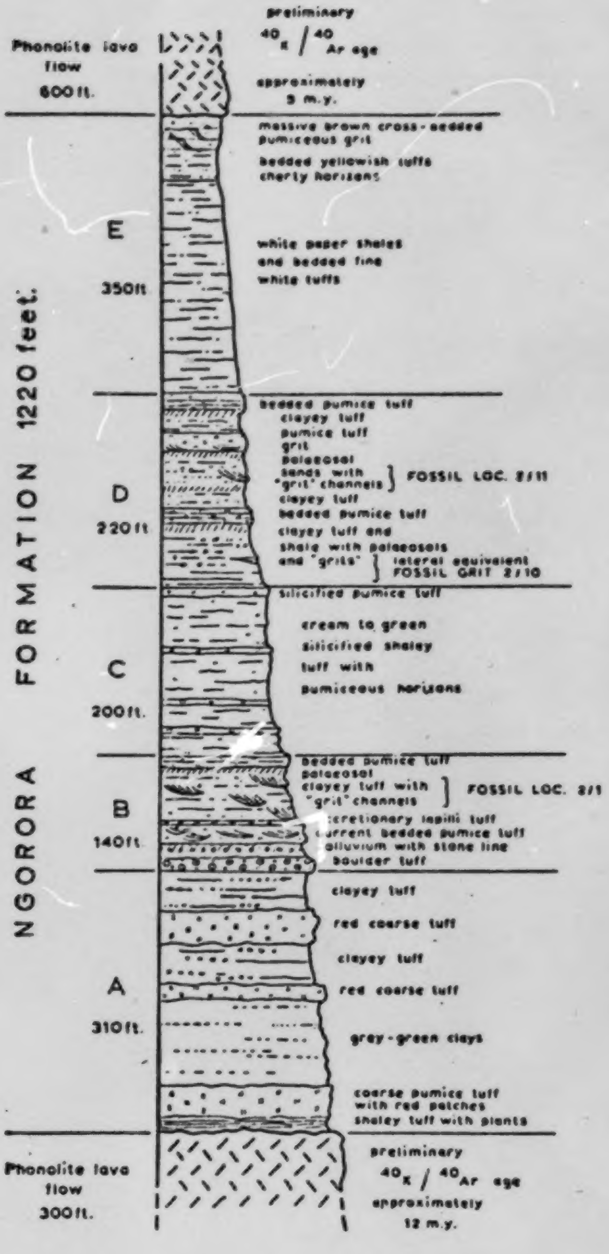
Hominid remains (KNM-CH 1) consist of most of the right facial skeleton togehter with parts of the left facial skeleton, right frontal, and the right basal colvaria including the petrosal posteriorly. Upper right maxillary

Figure II - 25


N
Sidekh
6094'
Kinyach
Kabarsero
Chepkesin
Bartabwa
Kamuiton
6656'
Yatya
KERIO VALLEY
Poi
Sibillo
Saimo
8203'
KAMASIA (TUGEN) HILLS
Kabartonjo
Kapluk
TIPARAINA RANGE
0 Miles 5
to Nakuru
to Nginyang
Loruk
Lake Baringo
Kampi ya Samaki
ETHIOPIA
UGANDA
KENYA
SOMALIA
map area
Kisumu
Nairobi
TANZANIA
Mombasa
Indian Ocean
Ngorora Fm.
Chemeron Beds

Map of the Lake Baringo area, Kenya, showing the distribution of the Ngorora formation and Chemeron Beds. (From Bishop and Chapman (1970):916)

Figure II - 26


NGORORA FORMATION 1220 feet.
Phonolite lava flow
600 ft.
preliminary
$^{40}K/^{40}Ar$ age
approximately
9 m.y.
E
350 ft
massive brown cross-bedded pumiceous grit
bedded yellowish tuffs
cherty horizons
white paper shales
and bedded fine
white tuffs
D
220 ft
bedded pumice tuff
clayey tuff
pumice tuff
grit
palaeosol
sands with "grit" channels
FOSSIL LOC. 2/11
clayey tuff
bedded pumice tuff
clayey tuff and
shale with palaeosols
and "grits"
lateral equivalent
FOSSIL GRIT 2/10
C
200 ft.
silicified pumice tuff
cream to green
silicified shaley
tuff with
pumiceous horizons
B
140 ft.
bedded pumice tuff
palaeosol
clayey tuff with "grit" channels
FOSSIL LOC. 2/1
accretionary lapilli tuff
current bedded pumice tuff
colluvium with stone line
boulder tuff
A
310 ft.
clayey tuff
red coarse tuff
clayey tuff
red coarse tuff
grey-green clays
coarse pumice tuff
with red patches
shaley tuff with plants
Phonolite lava flow
300 ft.
preliminary
$^{40}K/^{40}Ar$ age
approximately
12 m.y.

Simplified stratigraphic sequence of the Ngorora Succession, Lake Baringo, Kenya.
(From Bishop and Chapman (1970):916)

dentition $C \rightarrow M^3$ are intact. Affinities of the specimen are with *Australopithecus robustus* in the size and massiveness of the face, buccolingually expanded cheek teeth, and a broad dished face.

Endocranially the specimen appears to have possessed much larger anterior and middle cranial fossae than is seen in Olduvai Hominid 5 or SK 1585, and much larger than in the available specimens of *A. africanus*. A rough estimate of the endocranial colume is given at more than 530 cc. The specimen is the youngest known representative of the large form of Australopithecus which shows, however, many features such as enlarged cranial capacity, face positioned more below the brow case, and reduction of the size of the temporalis muscle suggesting morphological advances in the direction which lead to the genus *Homo* in other lineages.

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GEOLOGY AND DISCOVERIES OF THE AFAR TRIANGLE

The Afar Triangle or Afar Depression comparises parts of different Ethiopian Provinces of Erythrea, Tigrai, Wallo and Harrar as well as the French Territory of the Afars and the Issas (T.F.A.I.). The depression has been investigated by French geologists since 1967, although earlier explorations had been undertaken since 1814.

The entire region has been subdivided and described in two parts. The northern half of the depression has been called the "Danakil" Depression and begins with a northern apex in the Gulf of Zula, Red Sea. The "Danakil" is bounded to the west by the Ethiopian highlands and the escarpment, and to the east by the Danakil Alps.

The southern continuum of the Afar Triangle includes the Central Afar Region and the T.F.A.I. The base of the triangle is demarcated by the Somali Plateau. Throughout the area volcanic and sedimentary formations from Miocene through Quaternary in age are to be seen interbedded with each other.

From earliest Miocene,volcanic activity has been continuous within the Depression. The volcanic unit referred to as the "stratoid series" is characterized by flood basalts and rhyolites (acidic lavas) and as a unit covers a time interval from at least 4 million years up to recent Quaternary.

The sedimentary sequence for the northern Afar consists of the following deposits: (1) the oldest sediments of detrital composition are referred to as the polychromatic formations (Mio-Pliocene), yielding as yet no fossiliferous localities, (2) Piedmont continental formations (Pleistocene), (3) marine limestones (Middle Pleistocene), and three additional formations ranging from Middle Pleistocene to recent times.

The Piedmont continental formations are represented in large alluvial fans composed of supposedly torrential conglomerates. Fans representing older depositions encase one another; the older the fan the more inclined is the average slope of the fan surface.

Different industries have been found and have approximated a date for many of the surface levels ranging from Acheulean to Mousterian to Neolithic. The exact sequence and chronology are difficult to establish and must await detailed local analysis.

Fossil hominid discoveries have been reported for the central Afar Depression along the Awash River in a zone ranging between the parallels 11°40' and 10° North. The Awash River flows from the south to the north along a longitude approximating 40°30' East, and the basin which it produces is limited to the west by the Ethiopian escarpment and to the northeast by the Magenta Plateau. This plateau is comprised of a series of volcanics belonging to the end of the Miocene through the Pliocene. Four sedimentary deposits belong to the Plio-Pleistocene age,the Central Afar Group are referred to as the Hadar Formation, the Meschelle Formation, the Leadu Formation and the Haouna-Lédi Formation.

The Hadar Formation is over 80 meters in thickness and is comprised of seven cyclical units labeled A through G. Unit A is associated with a volcanic ash deposit and Unit D is associated with a basalt deposit. Mammalian fossil assemblages have been collected from Units A, B, D and E.

The Meschelle Formation is about 150 inches in thickness and is comprised of some nine units labeled A through I. The remaining two formations are less extensive. The faunal assemblages from Haouna-Lédi and Leadu are comparable to those from the deposits of the Omo labeled D. E. F and lower H from the Shungura Formation, situated in time between 2 and 3 million years.

The fossiliferous localities of the Hadar Formation are perhaps a little older, equivalent to Zone 5 of the biostratigraphic units of Coppens. In absolute chronology this indicates an age of about 4.0 million years and is equivalent to series A-C of the Shungura Formation at Omo.

During the field season of 1973, three localities have yielded hominid fossil remains in the region of Hadar, to the north of the Awash River. This area is some 150 Km^2 and has already produced eighty-nine additional fossiliferous localities. The Awash River cuts through sedimentary deposits formed by lake systems. The succession is well stratified on a horizontal plane. The Hadar area is an eroded gully system into the main river. Radiometric determinations on volcanic basalt have yielded dates of 3.0 million years.

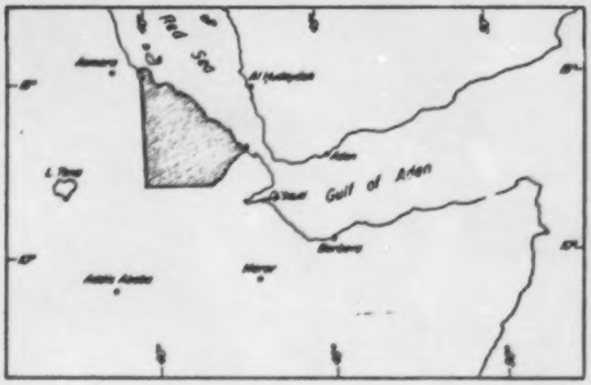
From locality AL 129, a sandstone ravine, the first hominid specimen was recovered on the surface and consisted of a distal femur and a proximal tibia. The femur is notable for its marked angle of the shaft yet the size is similar to that of a chimpanzee. At this same locality an additional right proximal femoral end was collected. A fragment of a left proximal femur was also collected some 80 meters away (Locality 128) but probably belonged to the same individual. 500 meters (Locality 166) from these postcranial fragments, a fragment of a left temporal including the external auditory meatus was found and anatomically resembles that of the robust form of australopithecus. The long bones are more reminiscent of those of A. africanus.

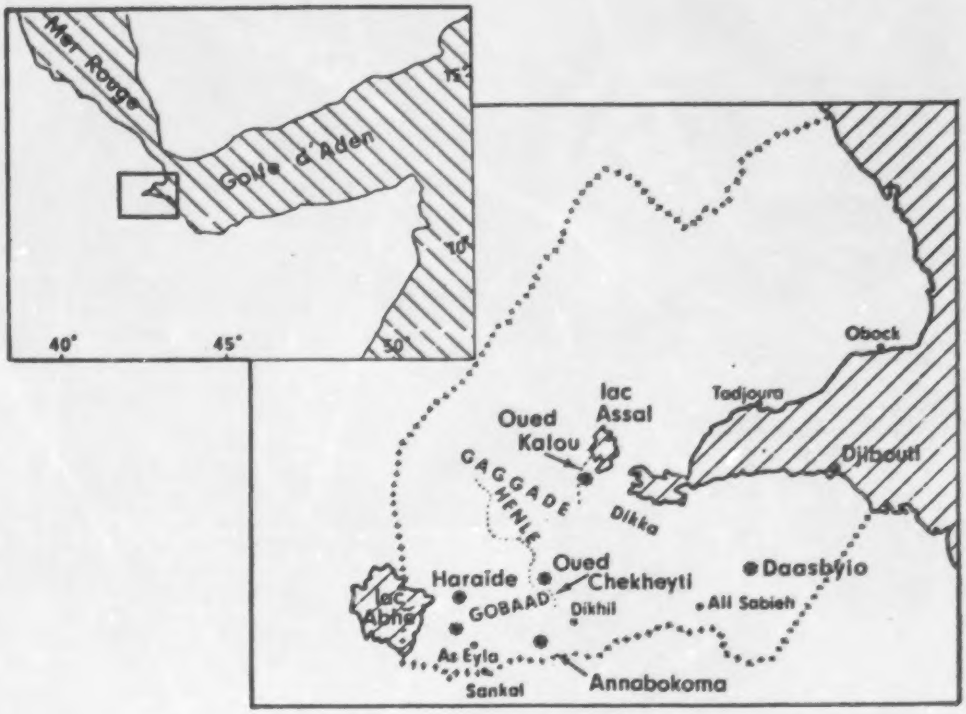
More recently the Afar Research Expedition during 1974, led by French scientists M. Taieb, Y. Coppens and an American, D. Johanson, has reported the discovery of humen skeletal remains of an alleged female gracile australopithecine at Afar Locality 288. The remains consist of nearly 40 percent of the skeleton representing the hand, wrist, right arm, leg, mandible and cranial fragments, and one-half of the pelvis with an articulating sacrum. Nicknamed "Lucy", the skeleton represents the most complete discovery of an early hominid from the Plio-Pleistocene period.

The pelvis appears to be that of a female with a large sciatic notch and subpubic angle. The shoulder, elbow and hip joints are intact. The left femora measures 270-280 mm and, compared to the humerus, is relatively short. It is proposed that the forelimbs must have been somewhat larger compared to the hindlimbs than in modern hominids.

The jaw and teeth resemble that of the australopithecine but with some differences. The incisors are relatively small but the canine is large and possibly slightly projecting. The first lower premolar resembles the sectorial shape and the mandible is V-shaped.

Figure II - 27

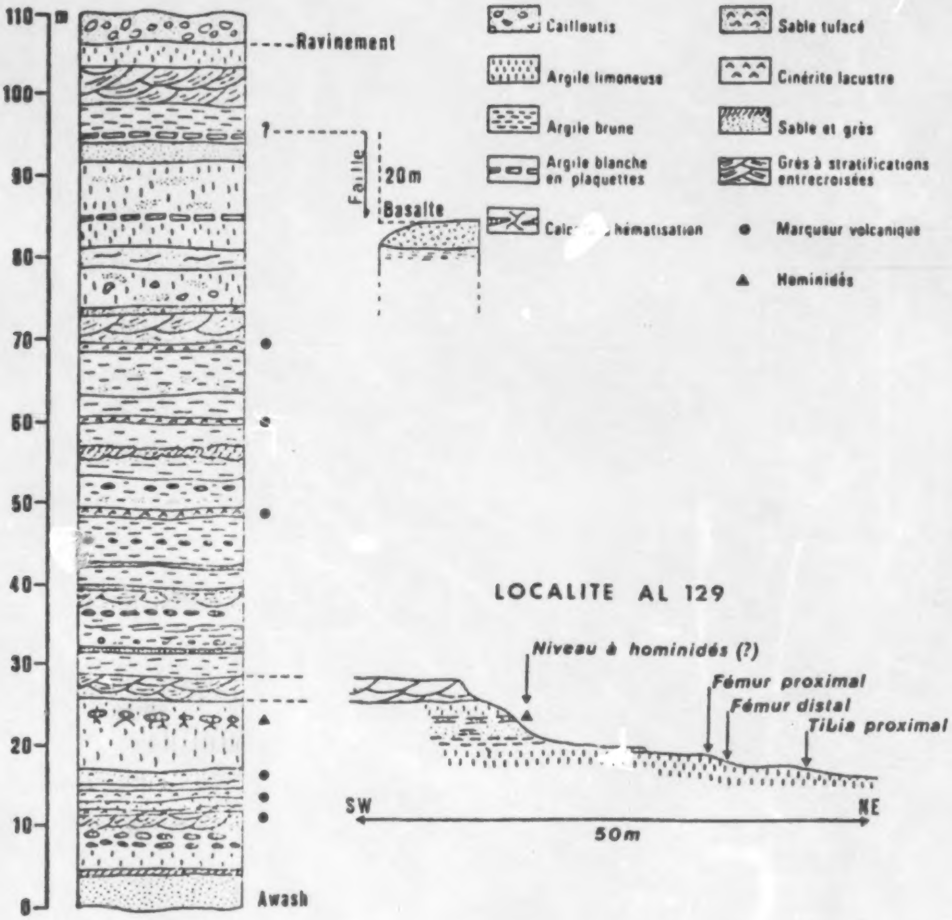

Red Sea
Gulf of Aden


Mer Rouge
Golfe d'Aden
15°
10°
40°
45°
50°
Obock
Tadjoura
lac Assal
Oued Kalou
Djibouti
GAGGADE
HENLE
Dikka
Oued Chekheyti
Daasbyio
Haraïde
lac Abhe
GOBAAD
Dikhil
Ali Sabieh
As Eyla
Sankal
Annabokoma

Above. Outline map of the Northern Afar, "Danakil" Depression.
(From the CNR-CNRS Research Team (1973):445)

Below. Map of Territory of Afars and Issas. Eastern Afar Depression.
(From Roger et. al. (1974):329)

Figure II - 28


110
m
100
90
80
70
60
50
40
30
20
10
0
Ravinement
?
Faille
20m
Basalte
Awash
Cailloutis
Argile limoneuse
Argile brune
Argile blanche en plaquettes
Calc[illegible] hématisation
Sable tufacé
Cinérite lacustre
Sable et grès
Grès à stratifications entrecroisées
Marqueur volcanique
Hominidés
LOCALITE AL 129
Niveau à hominidés (?)
Fémur proximal
Fémur distal
Tibia proximal
SW
NE
50m

Simplified stratigraphic column of the Hadar region, Central Afar Awash Basin. Locality AL 129 showing position of hominid fossil remains.
(From Taieb et. al. (1974):736)

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1974 Découverte d'hominidés dans les series Plio-pléistocènes d'Hadar (Bassin de l'Awash, Afar, Éthiopie). C. R. Acad. Sci. (Paris) 279D: 735-738.

Describes the discovery of five fragments of human postcranial and cranial bones from the Hadar locality, Awash Basin, and dates this locality by faunal association to between 3 and 4 million years.

FAUNAL ZONES IN EAST AFRICA

Reference: Coppens, Y. 1972.
C. R. Acad. Sci. 274: 181-184.

Zone VIII	Represented by the fauna from the Lukeino and the Mpesida of the Lake Baringo Basin.
Zone VII	Represented at Lothagam 1 and the Kaperyon Beds, characterized by *Stegotetrabelodon* *Primelephas*, *Nyanzachoerus archaique*, *Hippopotamus hexaprotodon*, *Dinotherium*, *Stylohipparion*, *Hipparian*, *Anancus*, *Australopithecus*.
Zone VI	Represented at Kaiso 1 and characterized by the persistence of *Primelephas*, *Hipparion*, *Anancus*, *Stegodon*, *Nyanzachoerus*, *Hippopotamus hexaprotodon* and in the contemporary deposits at Omo O, Kanapoi, Lothagam 3, Kubi Alga, Chemeron, Kanam, *Stegotetrabelodon*, *Dinotherium*, *Stylohipparion*, *Libyatherium* and *Australopithecus*.
Zone V	Represented at Omo (Shungura A, B, C, D); characterized by *Stegodon*, *Nyanzachoerus*, *Hippopotamus hexaprotodon*, *Dinotherium*, *Stylohipparion*, *Libyatherium*, *Elephas*, *Australopithecus* and the disappearance of *Primelephas* and *Anancus*.
Zone IV	Represented at Omo (Shungura D, E, F, G, lower H); characterized by *Hippopotamus hexaprotodon*, *Dinotherium*, *Stylohipparion*, *Libyatherium*, *Elephas*, *Australopithecus* and the disappearance of *Stegodon* and *Nyanzachoerus*.
Zone III	Represented at Olduvai Gorge Bed I and Lower Bed II; characterized by *Dinotherium*, *Stylohipparion*, *Libyatherium*, *Elephas*, *Australopithecus*, *Equus* and *Homo*, with the disappearance of *Hippopotamus hexaprotodon*.

Zone II	Represented at Olduvai Gorge Upper Bed II; characterized by the disappearance of *Dinotherium*.
Zone I	Characterized by the disappearance of *Australopithecus*, *Stylohipparion* and *Libyatherium*.

EAST RUDOLF SUBSEQUENCE

FAUNAL ZONE

Reference: V. Maglio. 1972.
Nature 239 (5372): 379-385.

Zone 4 "*Notochoerus capensis* Zone".

Represented at the Kubi Alga Beds and characterized by *Elephas ekorensis*, *Notochoerus capensis*, *Nyanzachoerus* sp. and early *Hippopotamus* sp.

Zone 3 "*Mesochoerus limnetes* Zone".

Represented at the Lower Member, Koobi Fora Formation and characterized by *Elephas recki* stage 2, *Notochoerus enilus* (progressive), *Mesochoerus limnetes* (typical), *Ceratotherium simum* (early), *Hippopotamus* sp. nov. (early), and *Tragelaphus nakuae*.

Zone 2 "*Metridiochoerus andrewsi* Zone".

Represented in the Upper Member, Koobi Fora Formation and characterized by *Elephas recki* stage 3, *Mesochoerus limnetes* (progressive), *Metridiochoerus andrewsi* (typical), *Hippopotamus* sp. nov. (typical), *Ceratotherium simum* (progressive), *Tragelaphus* cf. *grandis*.

Zone 1 "*Loxodonta africana* Zone".

Represented in the Ileret Member and characterized by *Elephas recki* stage 3-4, *Loxodonta africana*, *Mesochoerus limnetes* (very progressive), *Metridiochoerus andrewsi* (progressive), *Hippopotamus* cf. *amphibius*, *Ceratotherium simum* (very progressive).

C. Problems in Dating: The Fossil Mammalian Fauna

MAMMALIAN FAUNA LISTS

EAST AFRICA
(excluding Hominidae)

General reference: Bishop, W.W. 1972: 240-244.

A. ALENGERR BEDS
Age: greater than 12.5 million years and less than 14 million years.

Proboscidea	
Deinotheriidae	*Deinotherium* c.f. *hobleyi* Andrews
Gomphotheriidae	
Perissodactyla	
Rhinocerotidae	*Dicerorhinus* *leakeyi* Hooijer

B. NGORORA FORMATION
Reference: Bishop & Chapman 1970—sediments and fauna described.
Age: probably just less than 12 million years or a little younger (certainly greater than 9 million years).

Primates	
Cercopithecoidea	
Carnivora	
Proboscidea	
Deinotheriidae	*Deinotherium* *hobleyi* Andrews
Gomphotheriidae	
Hyracoidea	sp. nov.?
Perissodactyla	
Rhinocerotidae	*Chilotherium* sp. *Aceratherium* sp. (? *D.* *leakeyi* Hooijer) *Brachypotherium* sp.
Artiodactyla	
Suidae	
Hippopotamidae	
Giraffoidea sp.	
Giraffidae sp.	
Bovidae	
Boselaphini	*Protragocerus* sp.
Tragelaphini/Boselaphini sp.	
Cephalophini/Boselaphini sp.	
Caprinae/Alcelaphini sp.	

C. MPESIDA BEDS
Reference: Maglio 1970—Elephantidae
Age: 7 ± million years.

Proboscidea	
Elephantidae	*Stegotetrabelodon* *orbus* Maglio
Perissodactyla	
Equidae	aff. *Hipparion*
Rhinocerotidae	
Artiodactyla	
Hippopotamidae	*Hippopotamus* sp.
Bovidae	

D. LUKEINO BEDS

Reference: Pickford, 1975.
Age: less than 6.7 million years--5.4 million years.

Carnivora	
Felidae	large sp.
	small sp.
Canidae	indet.
Viverridae	cf. *Ichneumia* sp.
Hyaenidae	cf. *Crocuta* sp.
Mustelidae	*Enhydriodon* cf. *iluecai*
Proboscidea	
Elephantidae	*Stegotetrabelodon orbus*
	Primelephas gomphotheroides
Perissodactyla	
Equidae	*Hipparion turkanense*
	cf. *sitifense*
Rhinocerotidae	2 spp.
Chalicotheriidae	undet.
Artiodactyla	
Suidae	*Nyanzachoerus tulotos*
Hippopotamidae	*Hippopotamus* sp.
Bovidae	*Reduncini* indet.
	Antilopini indet.
	Gazellini indet.
	Neotragini indet.
	Tragelaphini undet.
Giraffidae	*Giraffa* cf. *jumae*

E. KAPERYON BEDS

Reference: Maglio 1970: Elephantidae
Age: probably a little older than 5 million years.

Proboscidea	
Elephantidae	*Stegotetrabelodon orbus* Maglio
	Primelephas gomphotheroides Maglio
Perissodactyla	
Equidae	aff *Hipparion*
Artiodactyla	
Suidae	
Hippopotamidae	*Hippopotamus* sp.
Bovidae	
Rodentia	
Histricidae	

F. KANAPOI

Reference: Cooke and Maglio 1972.
Age: approximately 4.0 million years.

Suidae	*Nyanzachoerus* species B
	Nyanzachoerus species A
	Notochoerus capensis
	Notochoerus euilus
Elephantidae	*Loxodonta adaurora*
	Elephas ekorensis

G. LOTHAGAM GROUP I

Reference: Patterson, Behrensmeyer, Sill (1970)
Age: greater than 3.7 million years and less than 8.3 million years.

Primates		
	Cercopithecidae	indet.
Carnivora		
	Hyaenidae	indet. cf. *Civettictis*
	Felinae	indet. (a large form)
	Machairodontinae	indet.
Proboscidea		
	Gomphotheriidae	indet. *Stegotetrabelodon orbus*
		Primelephas gomphotheroides
		Loxodonta adaurora
Perissodactyla		
	Equidae	*Stylohipparion* sp.
Artiodactyla		
	Suidae	*Nyanzachoerus* spp. nov. A, B and C
Hippopotamidae		*Hippopotamus* (Hexaprotodon) spp. nov. A and B
Giraffidae		*Giraffa* sp.
Bovidae		*Tragelaphus* sp. cf. *T. nakuae*
		Gazella sp.
		Redunca sp. aff. *R. ancyatrocera*
Tubulidentata		
	Orycteropodidae	gen. et. sp. nov. *Deinotherium* sp.
Rodentia		
	Anomaluridae	nov.

H. ATERIR BEDS

Reference: Maglio 1970—Elephantidae
Age: slightly less than 4.2 ± 0.2 million years.

Proboscidea		c.f.	*Anancus* sp.
			Mammuthus subplanifrons Osborn
Perissodactyla			
	Equidae	aff.	*Hipparion*
	Rhinocerotidae		*Ceratotherium* sp.
Artiodactyla			
	Suidae	c.f.	*Sus* sp.
			Nyanzachoerus sp. B
Hippopotamidae			*Hippopotamus* sp.

I. KARMOSIT

Locality discovered and initial collections made by Dr. J. G. McCall.
Age: 3.4 ± million years (or a little older).

Proboscidea			
Perissodactyla			
	Rhinocerotidae		
Artiodactyla			
	Suidae		*Notochoerus euilus* Hopwood
	Hippopotamidae		*Hippopotamus* sp.
	Giraffidae		
	Bovidae		
		Tragelaphini	
		Reduncini	
		Antilopini	c.f. *Aepyceros* sp.

J. OMO BASIN, LAKE RUDOLF

References: Butzer 1971
Cooke and Maglio 1972
Coryndon and Coppens 1973
Howell, Fichter and Eck 1969

Age: about 4.0 million years (Mursi Formation) to 1.0 million years (upper Shungura Formation).

		Mursi	Usno	Shungura lower	Shungura upper
Primates					
Cercopithecidae	*Papio* sp.		x		
	Parapapio sp.		x		
	Simopithecus sp.		x		
	Cercopithecinae sp.		x		
	Colobus sp.		x		x
Carnivora					
Hyaenidae	indet.		x	x	
	Crocuta crocuta		x	x	
Canidae	indet.		x		
	Canis sp.			x	
	Lycaon sp.			x	
Felidae	indet.		x		
	Panthera cf. *leo*		x	x	
Machairodontidae	indet.		x		
Mustelidae	*Enhydriodon* sp.			x	
Proboscidea					
Elephantidae	*Elephas recki* stage 1		x	x	
	Dinotherium bozasi	x	x	x	
	Loxodonta adaurora	x		x	
	Elephas recki stage 2				x
Perissodactyla					
Equidae	*Stylohipparion* sp.		x	x	x
	Stylohipparion albertense	x			
Rhinocerotidae	*Diceros bicornis*		x	x	
	Ceratotherium simum		x	x	
Artiodactyla					
Suidae	*Nyanzachoerus* sp. A	x			
	Nyanzachoerus sp. B	x			
	Nyanzachoerus sp.		x		
	Nyanzachoerus kanamensis			?	
	Notochoerus capensis			x	
	Notochoerus scotti				x
	Notochoerus euilus		x	x	
	Mesochoerus heseloni		x		
	Mesochoerus limnetes			x	x
	Pronotochoerus jacksoni			x	x
	Metridiochoerus andrewsi				x
Hippopotamidae (reference: Coryndon and Coppens 1973)					
	Hippopotamus protamphibius (early through typical)	x	x	x	x

		Mursi	Usno	Shungura	
				lower	upper
	Hippopotamus sp. A		x	x	x
	Hippopotamus cf. *amphibius*				x
	Hippopotamus sp. B			x	x
Giraffidae	*Libyatherium*			x	
	Giraffa gracilis		x	x	
	Okapia sp.		x	x	
Camelidae	*Camelus* sp.			x	x
Bovidae	*Redunca ancystrocea*			x	
	Bovini sp.			x	
	Tragelaphine sp.	x			
	Tragelaphus nakuae		x	x	
	Menelikia				x
	Kobus sigmoidalis		x	x	
	Gazella praethomsoni				x
	Alcelaphini indet.		x	x	
	Aepyceros sp.		x	x	
Tubulidenta	*Orycteropus* sp.		x	x	
Rodentia	*Hystrix* sp.		x	x	

K. CHEMERON FORMATION

References: Martyn 1967—sediments (including comments on fauna by L. S. B. Leakey)
Leakey, R. E. F. 1969—Cercopithecidae
Hooijer 1969—Rhinocerotidae
Maglio 1970—Elephantidae

Age: greater than 2.0 million years and less than 5.4 million years.

Primates		*Papio baringensis* Leakey
		Paracolobus chemeroni Leakey
Proboscidea		*Deinotherium bozasi* Arambourg
		Anancus sp.
		Mammuthus subplanifrons Osborn
		Loxodonta adaurora Maglio
		Elephas recki stage 2 Dietrich
Perissodactyla		
Equidae	aff.	*Hipparion*
Rhinocerotidae		*Ceratotherium simum* Burchell
Artiodactyla		
Suidae		*Nyanzachoerus* sp. 'A'
		Nyanzachoerus sp. 'B' or *Mesochoerus* c.f. *heseloni* Leakey
	c.f.	*Mesochoerus* sp.
	c.f.	*Sus* sp.
	c.f.	*Potamochoerus* sp.
Hippotamidae		*Hippopotamus* c.f. *imagunculus* Hopwood
		Hippopotamus sp. nov.
Giraffidae		
Sivatheriinae		
Bovidae		
Tragelaphini		
Alcelaphini		
Rodentia		
Hystricidae		c.f. *Xenohystrix crassidens*

L. EAST LAKE RUDOLF

Reference: Maglio 1972

Age: Radiometric determinations of the KBS Tuff are being revised. Dates range from 2.6 million years to 1.5 million years.

		Ileret	Koobi Fora	Kubi Alga
Primates				
Cercopithecidae	Cercocebus cf. ado	x	x	
	Cercopithecus sp. indet.	x	x	
	Colobus sp.	x	x	
	Colobinae gen et sp. indet.		x	
	cf. Papio sp.		x	
	Simopithecus sp.	x	x	
Carnivora				
Hyaenidae	Crocuta cf. crocuta	x	x	
	Hyaena cf. hyaena	x	x	
Canidae	Canis cf. mesomeles	x	x	
Felidae	Panthera sp.	x	x	
	cf. Therailurus sp.	x		
	cf. Homotherium sp.		x	
	Megantereon eurynodon	x	x	
Mustelidae	Lutra sp.	x	x	
Viverridae	gen et sp. indet.	x		
Proboscidea				
Deinotheriidae	Deinotherium bozasi	x	x	
Elephantidae	Elephas ekorensis			x
	Elephas recki stage 2, 3	x	x	
	Loxodonta adaurora		x	x
	Loxodonta africana	x		
Gomphotheriidae	Anancus sp.			x
Perissodactyla				
Equidae	Equus sp.	x	x	
	Hipparion cf. albertense	x	x	
Rhinoceratidae	Ceratotherium simum	x	x	
	Diceros bicornis	x	x	
Artiodactyla				
Bovidae	Damaliscus sp. nov.	x	x	
	Damaliscus cf. niro	x	x	
	Connochaetes cf. africanus	x		

		Ileret	Koobi Fora	Kubi Algi
	Megalotragus cf. *kattwinkeli*	x	x	
	Aepyceros sp.	x	x	
	Antidorcas wellsi		x	
	Gazella sp. indet.		x	
	Pelorovis cf. *olduwayensis*	x		
	Pelorovis sp. nov.	x	x	
	cf. *Synceros* sp.			x
	Hippotragus gigas	x		
	Oryx sp.	x		
	Kobus sigmoidalis	x	x	
	Kobus cf. *kob*	x	x	
	Menelikia sp.	x	x	
	Redunca ancystocera	x	x	
	Tragelaphus nakuae		x	
Giraffidae	*Sivatherium* sp. nov.	x	x	
	Giraffa cf. *jumae*	x	x	
	Giraffa sp. (=cf. *stillei*)	x	x	
	Giraffa cf. *gracilis*	x	x	
Suidae	*Mesochoerus limnetes*	x	x	
	Metridiochoerus andrewsi	x	x	
	"*Pronotochoerus jacksoni*"	x	x	
	Notochoerus capensis			x
	Notochoerus euilus		x	
	Notochoerus scotti		x	
	Nyanzachoerus sp.			x
	Potamochoerus sp.	x		
	Phacochoerus cf. *aethiopicus*	x	x	
	cf. *Afrochoerus nicoli*		x	
Hippopotamidae	*Hippopotamus* sp. nov.	x	x	
	Hippopotamus cf. *amphibius*	x	x	
	Hippopotamus aff. *imaguncululus*	x	x	x
Tubulidentata				
Orycteropodidae	*Orycteropus* sp.	x	x	
Rodentia				
Hystricidae	*Hystrix* sp.	x		
Thryonomyidae	*Thryonomys* sp.	x	x	

M. OLDUVAI GORGE

Reference: M. Leakey 1971

Age: less than 1.9 million years.

		Bed I		Bed II
		lower	upper	lower
Primates				
Lorisidae	*Galago senegalensis*		x	
	Galago sp.	x		
Cercopithecidae	*Simopithecus* cf. *oswaldi*	x	x	

		Bed I lower	Bed I upper	Bed II lower
	c.f. *Cercocebus* sp.	x		
	Papio sp.		x	
	Colobus sp.		x	
Indet.				x
Insectivora				
Erinaceidae	*Erinaceus broomi*		x	
Macroscelididae	*Nasilio* sp.		x	
	? *Elephantulus* sp.		x	
	Indet.		x	
Indet.			x	x
Soricidae	*Mysorex* cf. *robinsoni*		x	
	Crocidura cf. *hindei*		x	
	Suncus sp.		x	
	Suncus cf. *lixus*		x	
	Suncus cf. *orangiae*		x	
Chiroptera				
Megadermidae	Indet.		x	
Vespertilionidae	Indet.		x	
Carnivora (reference: Petter 1973)				
Canidae	*Canis mesomelas*		x	
	Prototocyon recki		x	
Mustelidae	*Aonyx* sp.	x	x	
Viverridae	*Herpestes* sp. aff. *ichneumon*		x	
	Galerella primitivus sp. nov.		x	
	Galerella debilis sp. nov.		x	
	Atilax sp.			x
	Ichneumia sp. aff. *albicanda*		x	
	Mungos dietrichi		x	
	Mungos minutus *sp.* nov.		x	
	Mungos sp.		x	
	Pseudocivetta ingens	x	x	
	Pseudicivetta ingens s. sp.			x
Hyaenidae	*Crocuta crocuta*	x	x	x
	Hyaena hyaena		x	x
Felidae	*Panthera leo* s. sp.		x	x
	Panthera pardus s. sp.		x	x
	Panthera crassidens		x	
	? *Machairodus* sp.			x
	? *Metailurus* sp.			x
Proboscidea				
Deinotheriidae	*Deinotherium* cf. *bozasi*	x	x	x
Elephantidae	*Elephas recki* stage 3		x	x
Hyracoidea				
Procavidae	Indet.	x		

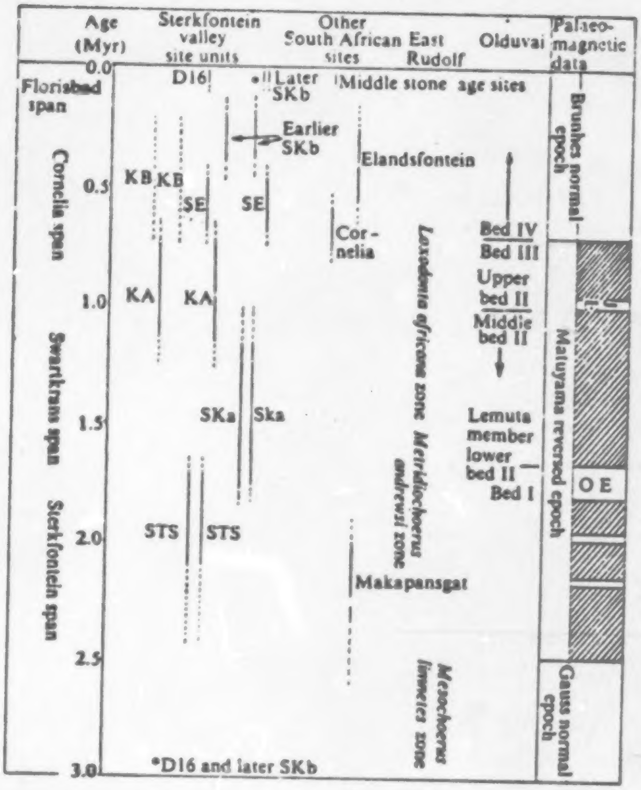
		Bed I lower	Bed I upper	Bed II lower
Perissodactyla				
Equidae	Equus cf. olduwayensis	x	x	x
	Stylohipparion sp.	x	x	x
Chalicotheriidae	Ancylotherium cf. hennigi	x		
Rhinocerotidae	Ceratotherium simum	x	x	x
	Diceros bicornis			x
Artiodactyla				
Suidae (reference: Cooke and Maglio 1972)				
	Mesochoerus olduvaiensis			x
	Mesochoerus dubius		x	x
	Phacochoerus antiquus		x	
	Pronotochoerus jacksoni		x	x
Hippopotamidae	Hippopotamus gorgops	x	x	x
Giraffidae	Giraffa jumae		x	x
	Giraffa gracilis			x
	Giraffa sp.	x	x	x
	Okapia sp.	x	x	
	Libyatherium olduvaiensis	x	x	x
Bovidae	Strepsiceros maryanus	x	x	x
	Strepticercos grandis			x
	Strepsicerotini indet.	x	x	x
	Pelorovis oldowayensis			x
	Bovini (small) indet.	x	x	x
	Kobus sigmoidalis		x	
	Kobus sp.	x	x	x
	Redunca sp.		x	
	Hippotragus gigas	x	x	x
	Oryx sp.		x	
	Hippotragini indet.		x	x
	Parmularius altidens	x	x	
	Xenocephalus sp.	x		x
	Beatragus antiquus		x	x
	Gorgon olduvaiensis		x	x
	Damaliscus angusticornis		x	
	Damaliscus niro			x
	Alcelaphini indet.	x	x	x
	Neotragini indet.		x	
	Gazella weilsi	x	x	x
	Phenacotragus recki			x
	Gazella sp.			x
	Antilopini indet.	x		x
	Pultiphagonides africanus			x
	Tribe indet. sp. nov.		x	
Rodentia				
Cricetidae	Tatera sp.		x	
Muridae	Otomys kempi		x	
	Gerbillus sp.		x	
	Saccostomus sp.		x	

		Bed I lower	Bed I upper	Bed II lower
	cf. *Grammomys* sp.		x	
	cf. *Steatomys* sp.		x	
	Dendromys sp.		x	
	Various		x	
Sciuridae	*Xerus* sp.		x	
Pedetidae	*Pedetes* sp.		x	
Hystricidae	*Hystrix* sp.	x	x	
Bathyergidae	*Heterocephalus* sp.		x	x
Lagomorpha				
Leporidae	*Serengetilagus* sp.		x	

N. CHESOWANJA
Reference: Carney, Hill, Miller and Walker 1971—sediments and fauna.
Age: probably less than 1.2 ± million years.

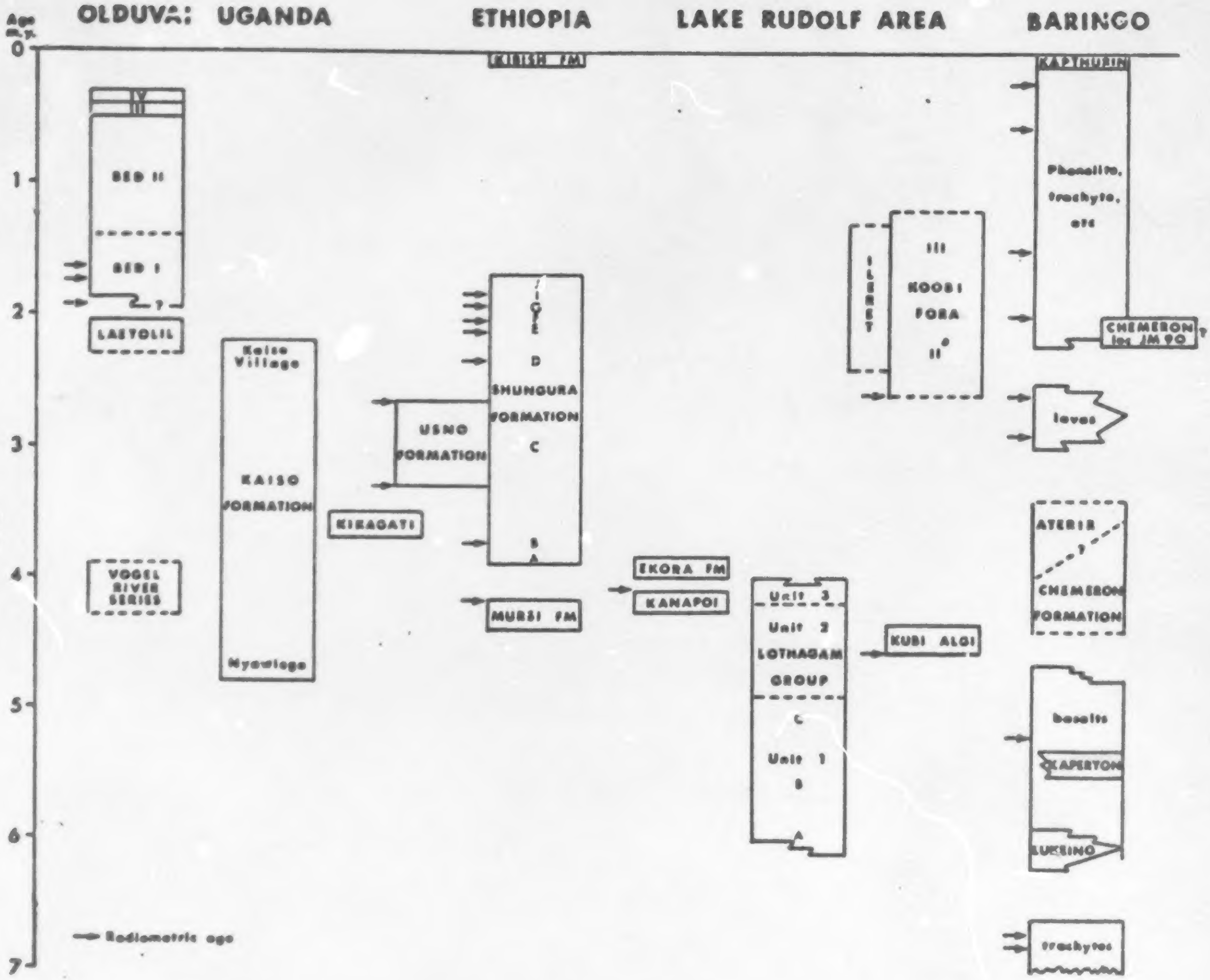
Primates	
Cercopithecidae	*Simopithecus* sp.
	sp indet.
Proboscidea	
Elephantidae	*Elephas* c.f. *recki* Dietrich
Deinotheriidae	*Deinotherium* *bozasi* Arambourg
Perissodactyla	
Equidae	*Equus* sp.
Rhinocerotidae	*Ceratotherium* sp.
Artiodactyla	
Suidae	*Pronotochoerus* *jacksoni* Leakey
	"*Metridiochoerus*" sp.
Hippopotamidae	*Hippopotamus* c.f. *amphibius* Linn
Giraffidae	
Bovidae	
Tragelaphini	*Tragelaphus* sp.
? Tragelaphini	
Bovini	
Reduncini	*Kobus* sp.
Alcelaphini	? *Megalotragus* *kattwinkeli* Schwarz
	? *Connochaetes* sp.
	small sp.
	smaller sp.
Antilopini	? *Antidorcas* sp.

Figure II - 29



Chronological relationships of the hominid bearing sites in South Africa based on the data of fossil bovids. Comparative data from East Rudolf and Olduvai Gorge, East Africa included.
J.E. = Jaramillo Event
O.E. = Olduvai Event
(From Vrba (1975):303)

Figure II - 30

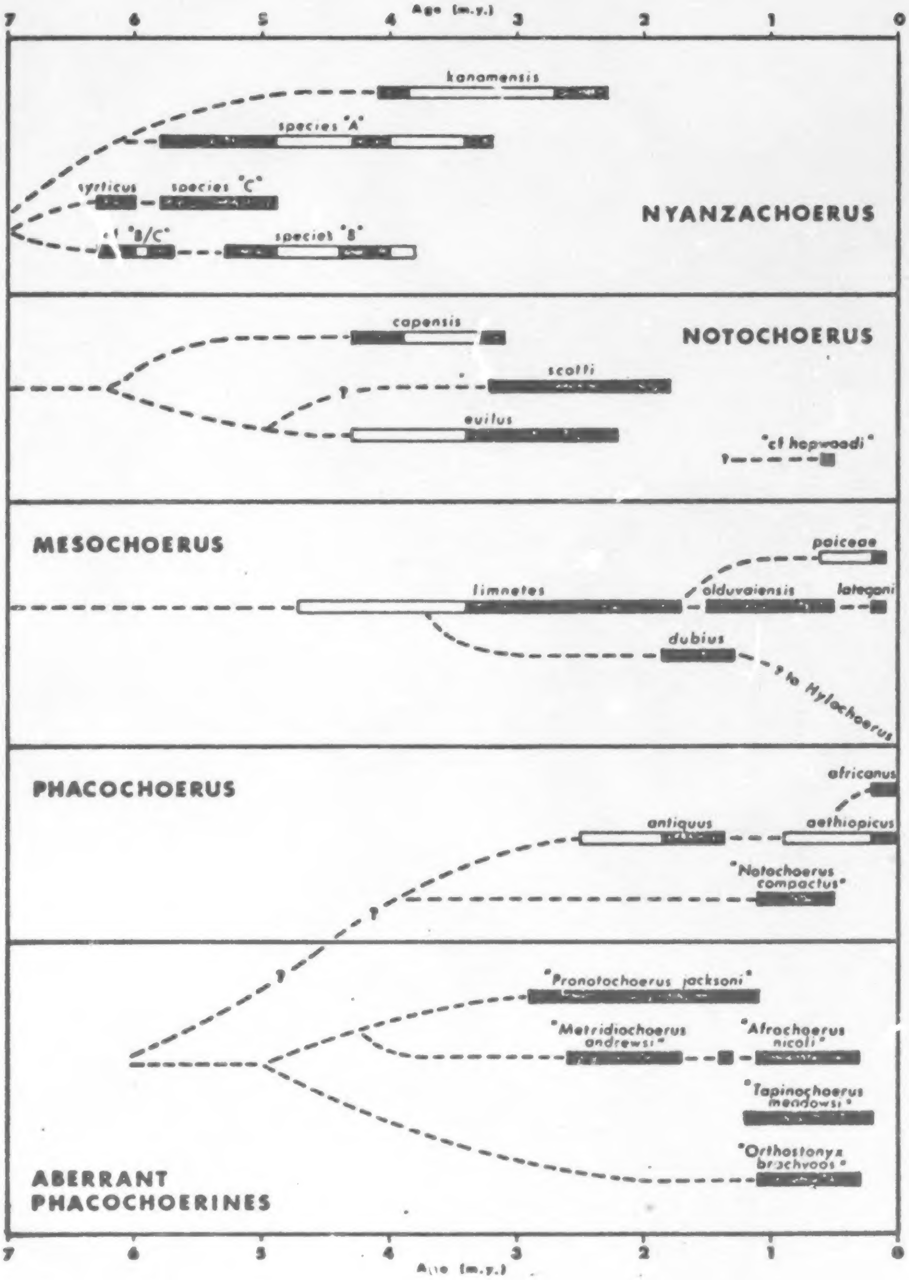


TENTATIVE CORRELATIONS OF PLIO/PLEISTOCENE DEPOSITS IN EAST AFRICA BASED ON PROBOSCIDEA AND SUIDAE.

(From Cooke and Maglio (1972): 306)

EVOLUTION OF FOSSIL SUIDAE IN AFRICA

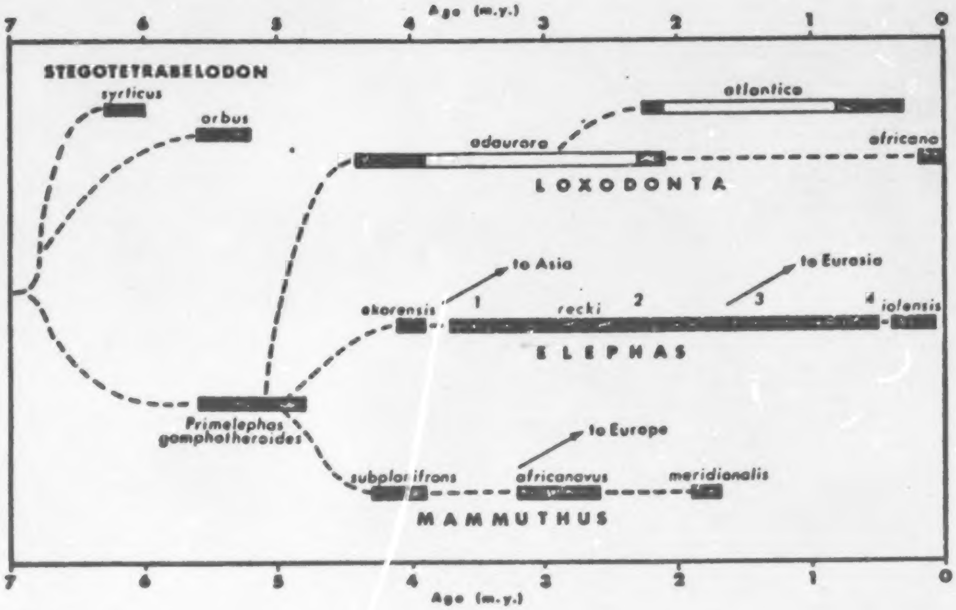
Figure II - 31



From Cooke and Maglio (1972): 308.

EVOLUTION OF FOSSIL ELEPHANTIDAE IN AFRICA

Figure II - 32


Age (m.y.)
7
6
5
4
3
2
1
0
STEGOTETRABELODON
syrticus
orbus
atlantica
adaurora
africana
LOXODONTA
to Asia
to Eurasia
ekorensis
1
recki
2
3
4
iolensis
ELEPHAS
Primelephas gomphotheroides
to Europe
subplanifrons
africanavus
meridionalis
MAMMUTHUS
Age (m.y.)

From Cooke and Maglio (1972): 319.

MAMMALIAN FAUNAL LISTS

SOUTH AFRICA
(excluding Hominidae)

General Reference: Brain 1958
Annals of Transvaal Museum 11: 129-130.

STERKFONTEIN TYPE SITE (STS)

Age: Sterkfontein Faunal Span, about 2.0 ± .5 million years.

Insectivora	
Myosorex robinsoni Meester	Meester 1955
Suncus Hemprich and Ehrenberg *sp.*	"
Chlorotalpa spelea Broom	Broom 1941
Elephantulus Thomas & Schwann *sp.* possibly = *E. langi* Broom	Broom & Schepers 1946
Primates	
Parapapio jonesi Broom	Freedman 1957
Parapapio jonesi Jones	"
Parapapio whitei Broom	"
Cercopithecoides williamsi Mollet	"
Proboscidea	
Elephantidae	
Elephas ekorensis	Maglio 1972
Carnivora	
Hyaena Brisson *sp.*	Ewer 1955a
Crocuta cf. *spelaea* (Goldf.)	"
Lycyaena silberbergi Broom	Ewer 1955b
? *Lycyaena nitidula* Ewer	"
Therailus barlowi (Broom)	Ewer 1955c
Megantereon gracile Broom	Broom 1948
? *Panthera pardus* (Linn.)	Ewer 1956b
Canis mesomelas Schreber sub-sp. *pappos* Ewer	"
Hydracoidea	
Procavia transvaalensis Shaw	Churcher 1956
Procavia antiqua Broom	"
Artiodactyla	
Tapinochoerus meadowsi (Broom)	Ewer 1956c
Metridiochoerus andrewsi	Maglio 1972

Bovidae (reference: Vrba 1974)

- *Hippotragus* cf. *equinus*
- cf. *Megalotragus* sp.
- *Redunca* cf. *arundinum*
- *Syncerus* cf. *acoelotus*
- *Tragelaphus* sp. aff. *angasi*
- cf. *Gazella vanhoepeni*

Makapania cf. broomi
cf. Hippotragus sp. aff. gigas
Oreotragus major
Antidorcas cf. recki
Antidorcas bondi ?
Taurotragus cf. oryx ?
Connochaetes taurinus lineage
Damaliscus sp.
medium-sized alcelaphines

Rodentia

Mystromys hausleitneri Broom (Broom 1948 puts this in a separate subspecies, barlowi, distinct from the Kromdraai form, but Lavocat 1956 does not think the separation is justified)	Broom 1948
Cryptomys robertsi Broom	Broom & Schepers 1946
Palaeotomys Broom sp.	Lavocat 1957
Dendromus Smith sp.	"
Dasymys Peters sp.	"
? Arvicanthis Lesson sp.	"
Mus minutoides Smith	"
Tatera Lataste sp.	"

MAKAPAN LIMEWORKS DEPOSIT

Age: Sterkfontein Faunal Span, about 2.0 million years and earlier.

Insectivora

Myosorex robinsoni Meester	Meester 1955
Suncus Hemprich & Ehrenberg sp.	"

Primates

Parapapio jonesi Broom	Freedman 1957
Parapapio broomi Jones	"
Simopithecus darti (Broom & Jensen)	"
Cercopithecoides williamsi Mollet	"

Carnivora

Hyaena makapani Toerien	Toerien 1952
Crocuta cf. brevirostris (Aym.)	"
Machaerodus darti Toerien = Therailuris	Toerien 1955
barlowi (Broom) according to	Ewer 1956a
Felidae indet.	"
Canis cf. adustus Sundevall	Ewer 1956c
Vulpes Frisch sp.	"
Cynictis penicillata (G. Cuv.) sub-sp. brachydon Ewer	Ewer 1956d

Hydracoidea

Procavia transvaalensis Shaw	Churcher 1956
Procavia antiqua Broom	"

Perissodactyla	
Stylohipparion van Hoepen sp.	Wells & Cooke 1956
Metaschizotherium (?) transvaalensis George	George 1950
? Ceratotherium Gray sp.	Wells & Cooke 1956
Diceros cf. bicornis (Linn.)	"
Artiodactyla	
Potamochoerides hypsodon Dale	Ewer 1958
Potamochoerides shawi (Dale)	"
Notochoerus euilus (Hopwood)	"
Notochoerus scotti	Maglio 1972
Bovidae (reference: Vrba 1974)	
? Redunca cf. arundinum	
? Syncercus cf. acoelotus	
? Tragelaphus sp. aff. angasi	
cf. Gazella vanhoepeni	
Makapania cf. broomi	
Hippotragus sp. aff. gigas	
Oreotragus major	
Hippopotamus makapanensis Kitching =	Kitching 1951
H. cf. amphibius Linn. according to	Wells & Cooke 1956
Giraffa cf. camelopardus Linn.	"
Griquatherium cf. cingulatum Haughton	"
Strepsiceros cf. strepsiceros (Pallas)	"
Strepsiceros (Tragelaphus) cf. angasi (Gray)	"
Taurotragus cf. oryx (Pallas)	"
cf. Syncerus caffer (Sparrman)	"
Cephalopus pricei Wells & Cooke	"
cf. Cephalopus (Guevei) caerulus (Hamilton Smith)	"
Redunca darti Wells & Cooke	"
Redunca cf. fulvorufula (Afzelius)	"
cf. Oryx gazella (Linn.)	"
Damaliscus sp. (aff. albifrons (Burchell))	"
cf. Gorgon taurinus (Burchell)	"
cf. Alcelaphus robustus Cooke	"
cf. Pelorocerus helmei (Lyle)	"
Makapani broomi Wells & Cooke	
Oreotragus major Wells	
Aepyceros cf. melampus (Lichenstein)	"
Gazella gracilior Wells & Cooke	"
Phenocotragus vanhoepeni Wells & Cooke	"
Rodentia	
Gypsorhyncus makapani Broom	Broom 1948
Xenohystrix crassidens Greenwood	Greenwood 1955
Hystrix major Greenwood	"
Hystrix cf. africae-australis Peters	"
Mystromys darti Lavocat	Lavocat 1956
Mystromys hausleitneri Broom	Lavocat 1957
Heterocephalus Ruppell sp.	"
Palaeotomys gracilis Broom	"
Malacothrix Wagner sp.	"
Dendromus Smith sp.	"

Dasymys Peters *sp.*	Lavocat 1957
Pelomys (?) Peters *sp.*	"
Lemniscomys (?) Trouessart *sp.*	"
Zelotomys (?) Osgood	"

SWARTKRANS (SKa)

Age: Swartkrans Faunal Span, about 1.5 ± .5 million years.

Insectivora

Myosorex robinsoni Meester	Meester 1955
Suncus Hemprich & Ehrenberg *sp.*	"

Primates

Parapapio jonesi Broom	Freedman 1957
Papio robinsoni Freedman	"
Simopithecus danieli Freedman	"
Dinopithecus ingens Broom	"
Cercopithecoides molleti Freedman	"

Hydracoidea

Procavia transvaalensis Shaw	Churcher 1956
Procavia antiqua Broom	"

Carnivora

Leecyaena forfex Ewer	Ewer 1955a
Hyaena brunnea Thunb. sub-sp. *dispar*. Ewer	"
Crocuta venustula Ewer	"
Crocuta crocuta (Erxl.) sub-sp. *angella* Ewer	"
Lycyaena silberbergi Broom	Ewer 1955b
Lycyaena nitidula Ewer	"
Therailurus Piveteau *sp.*	Ewer 1955c
Megantereon Cr. & Job. *sp.*	"
Nimravidae indet.	"
Panthera pardus (Linn.) sub-sp. *incurva* Ewer	Ewer 1956b
Panthera Oken *sp.* (Swartkrans "lion")	"
Canis mesomelas Schreber sub-sp. *pappos*	Ewer 1956c
Vulpes sp. ? = *V. pulcher* Broom	"
Cynictis penicillata (G. Cuv.)	Ewer 1956d
? = sub-sp. *brachydon* Ewer	Ewer 1956a

Artiodactyla

Tapinochoerus meadowsi Broom	Ewer 1956c
Phacochoerus antiquus Broom	"

KROMDRAAI FAUNAL SITE

Age: Latest Swartkrans Faunal Span → Cornelia Faunal Span, about 1.0 million years and later.

Insectivora

Suncus Hemprich & Ehrenberg *sp.*	Meester 1955
Chrysochloris, possibly *Proamblysomus antiquus* Broom	Broom 1948

Primates	
Parapapio jonesi Broom	Freedman 1957
Papio robinsoni Freedman	"
Papio angusticeps Broom	"
Gorgopithecus major Broom & Robinson	"
Carnivora	
Crocuta spelaea (Goldfuss) sub-sp. *capensis* Broom	Ewer 1954
Crocuta ultra Ewer	"
Hyaena bellax Ewer	"
Therailurus piveteaui Ewer	Ewer 1955c
Megantereon eurynodon Ewer	"
? *Epimachairodus* Kretzoi *sp.*	"
Felis crassidens Broom	Broom 1948
Kromdraai "lion" ? = *Panthera shawi* (Broom)	Ewer 1956b
Canis mesomelas Schreber sub-sp. *pappos* Ewer	Ewer 1956c
Canis atrox Broom	Broom 1939 & 1948
Vulpes pulcher Broom	Broom 1937
Herpestes mesotes Ewer	Ewer 1956d
? *Crossarchus transvaalensis* Broom	Broom 1939
Hydracoidea	
Procavia transvaalensis Shaw	Churcher 1956
Procavia antiqua Broom	"
Perissodactyla	
Equus sp. probably *E. zietsmani* Broom	Broom 1948
Artiodactyla	
Phacochoerus antiquus Broom	Ewer 1956c
Rodentia	
Mystromys hausleitneri Broom	Broom 1948 Lavocat 1956

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D. Problems in Interpretation: The Post-Cranial and Endocranial Evidence

EVIDENCE FROM THE POST CRANIAL MATERIAL

A comparison of the lists of hominid remains clearly demonstrates that the post cranial material is rather poorly represented in existing collections, but in general most anatomists agree that the early hominids were both upright in posture and bipedal rather than quadrupedal in gait.

Computation of stature of the australopithecines has used those techniques determined successful on modern populations. Until the Afar hominids and KNM ER 803 have been fully described, the single most complete specimen is STS 14 which includes all six lumbar vertebrae, sacrum, several ribs, femur, as well as the reconstructed pelvis. The small size and slender construction of the bones suggest a small-sized individual. Robinson (1972: 231) has estimated the height of this specimen based on the ratio between the sum of the lumbar vertebrae body lengths and stature in modern populations as well as estimated femur length. These estimates range from slightly below 4 feet (122 cm) to 4 feet 6 inches (137 cm). Much lower estimates have been calculated by Lovejoy and Heiple (1970) for the gracile australopithecines based on a reconstruction of the STS 14 femur and range between 107-109 cm (3'6" - 3'7").

The evidence for the robust australopithecine is not as good for estimating stature. The Swartkrans innominate (SK 50) is approximately 22 percent larger than that of STS 14 (Robinson 1972: 234). The Kromdraai innominate is of comparable size. Day (1973: 32-33) has reviewed the anatomical evidence of SK 50 and SK 3155b and believed that the acetabulum was small, that there was some backward extension of the ilium, that there was a marked area of attachment for the rectus femoris muscle with evidence of a reflected head, and that there was a marked ilio-psoas groove medial to the anterior inferior iliac spine. He states, however, that because of the condition of the specimen no anatomical measurements should be taken on this specimen.

There are no long bones of the robust australopithecines from South Africa sufficiently complete to provide an estimate of stature. The two femora from Swartkrans (SK 82, SK 97), however, are considerably more robust than the ones from Sterkfontein. Robinson (1972: 235) has suggested that by comparing the percentage differences in the post cranial bones that the robust form was slightly taller and perhaps moderately heavier. Estimates range from 4'6" (137 cm) to 5' (152 cm) in height and as much as 150-200 pounds in weight. The vertebrae suggest that the gracile males and the robust females may have been about the same size.

Burns (1971), using a ratio between femoral head diameter and body height in modern Homo sapiens, determined that body height was equal to 13.29 (femoral head diameter) + 108.59 cm. Using this equation, the height of SK 82 was determined to be 151 cm and that of SK 97 as 157 cm. Both estimates are within the range proposed by Robinson.

More recently, McHenry (1974) has proposed new height estimates based on regression analysis. He claims that values derived from the forelimb and hindlimb should not necessarily coincide since the limb proportions in australopithecines were probably different than in the modern forms. Estimates based on femora STS 14 and STS 34 yield a range between 4'3" (131 cm) and 4'10" (147 cm). If the STS humerus is included in the sample, the uppermost limit of the range is increased to 5'3" (159 cm). McHenry presumes that this variability in stature is related to sexual dimorphism. On the small sample of postcrania from Swartkrans and Kromdraai, the published range is much smaller--from 4'10" (148 cm) to 5'2" (157 cm). Comparisons of single bones, the humerus STS 7 and TM 1517, of different populations indicate how much size overlap exists between the South African forms.

Calculations of stature on the recently recovered femoral remains from East Africa, KNM ER 736, 737 and 738, have yielded much more valuable estimates. For the one species of Australopithecus represented by KNM ER 738 and 736, the range is respectively 4'11" (149 cm) to 6'1" (186 cm). Specimen KNM ER 737, attributed to the genus Homo, was estimated in height at 5'6" (168 cm). McHenry concludes that over time (from 4.0 to 1.3 million years) a trend of increasing size is discernable.

Lower Limbs

The two femoral fragments from Swartkrans (SK 82, SK 97) and the femur from Olduvai (OH 20) show similar morphological features in that all three display a groove for the obturator externus tendon on the posterior side of the femoral neck which functions in hyperextension and extension of the hip joint. Identification of an additional groove on the anterior aspect of the femoral neck for the tendon of the ilio-psoas muscle confirms that hip extension was habitual and not occasional (Day 1973: 35-36).

Certain discrete features of the femora are, however, unique to these specimens. The combination of a small head, long and relatively flat neck, non-flared greater trochanter and posteriorly directed lesser trochanter confirms the non-identity of these hominids with living groups (Day 1973: 36). Most of this diagnosis is confirmed by Lovejoy and Heiple (1972), who also demonstrate that the presence of the inter-trochanteric line, absent in some fossil specimens (OH 20) but not in others (STS 14, SK 82, SK 97), is to some extent related to age and even in modern adults its expression is highly variable. Lovejoy and Heiple (1972) refute the contentions, however, that the posteriorly directed lesser trochanter falls outside the range of modern human variation, or that the greater trochenters of the Olduvai and Swartkrans specimens are relatively smaller than in modern man. They assert that the more laterally placed shaft results in a merging of the greater trochanter into the proximal mass of the femur itself.

Two distal femora from Sterkfontein (STS 34 and TM 1513) show prominance of the lateral condyle in the region of the patellar groove. This is part of the mechanism in bipeds which counters lateral dislocation of the kneecap in full extension of the knee. Additionally, Day (1973: 37) describes the presence of asymmetrical grooves for the menisci on the flattened condylar surfaces as part of the knee-locking mechanism and the presence of grooving for the popliteal tendon in full flexion as part of the knee unlocking mechanism similar to that in modern hominids.

However, Preuschaft (1971), in analyzing the Olduvai specimens, believes that the relative slenderness of the Olduvai tibia and the stoutness of the fibula, the relative width of the medial femor condyle in comparison to the lateral and the contour of the patellar joint surface of the femur indicate the absence of the specialized human knee joint. The lateral border of the patellar joint is not elevated, which in turn prevents the patella from slipping laterally when the quadriceps muscle contracts in the modern hominid forms.

The Olduvai tibia and fibula shafts are described by Davis (1964: 967-968) and are essentially hominid in form except for certain characteristics. The shaft exhibits a more rounded anterior border similar to that in the Pongidae associated with an extension of tibialis anterior on the antero-medial surface of the bone in contrast to the sharp border seen in the modern forms. Midshaft the tibia shows greater extension for tibialis posterior than for flexor digitorum longus, again in contrast to Homo sapiens.

The upper tibia end appears to be intermediate between apes and man in the markings for popliteus muscle and the extent of attachment of soleus onto the tibia. Day (1973: 42), in his description of the KNM ER 803 tibia, states that the shaft is relatively straight and displays a strong area of attachment for the soleus muscle similar to the modern condition.

Preuchaft (1971: 238) suggests that the anteriorly tilted position of the distal tibial joint surface on the Olduvai specimen indicates a much more displaced center of gravity to the rear of the body.

Davis (1964: 967) remarks that the shaft of the Olduvai fibula is nearly identical to that of modern man the the apparent musculature is consistent with powerful plantor flexion of the foot.

The most complete foot bones are those of OH 8 which again show principal affinities with those of Homo sapiens. Described by Day and Napier (1964), Day (1967), and Day and Wood (1968), the presence of an articular facet between the bases of the first and second metatarsals demonstrates the absence of an opposable toe (Preuschaft 1971). However, the tilt of the talus, width of the horizontal talar neck angle, and the pattern of metatarsal robusticity, which may all be the results of individual variability, may also indicate that the striding gait of Homo sapiens had not yet been achieved.

In opposition to this idea, Archibald, Lovejoy and Heiple (1972) find the metatarsal pattern fully commensurate with a striding bipedal gait, that in many populations of modern forms substantial variability in relative robusticity exists and that this is immaterial to the gait pattern. Those features indicative of a striding gait are the very robust M-5 and the relatively reduced M-2. Day (1973: 42) notes that the third left metatarsal from KNM ER 803 is well developed dorsoventrally to withstand propulsive forces and is curved in torsion consistent with the formation of a transverse torsal arch.

More recently, Wood (1974) determined that the functional implications of canonical analysis which he performed on the fossil right talus from East Rudolf (KNM ER 813), attributed to the genus Homo, make it probably that the locomotor pattern of this particular specimen was like that of modern man, and in this his results differ from those of Day and Wood (1968) derived from the fossil talus (OH 8) from Olduvai. These differences may have phylogenetic significance.

Upper Limbs

The single clavicle fragment from Olduvai has been described by Napier (1965) who claimed that the clavicle was distinguishable from those of modern Homo sapiens by only slight differences. This position was criticized by Oxnard (1968) who examined the extent of clavicular torsion and claimed that it is much more similar to that in primates whose primary mode of locomotion is suspensory by the arms. In addition the medial end of the fragment is slightly modified to suggest that the scapulae were set relatively higher than in modern man.

Little evidence exists as to the proportion of upper limb length to lower limb length (see Afar Hominids). The incomplete humerus STS 7 is a robust and relatively long bone, and the suggestion has been made that the upper limb was slightly longer in proportion to the lower limb than is the case in modern man. The South African post cranial material, however, is not articulated except for perhaps TM 1517 from Kromdraai and it is impossible to determine if one limb bone belongs to the same individual as another. McHenry (1974: 335), however, is of the opinion, based on the post crania of Kromdraai TM 1517, that the humerus is proportionately much longer than that of modern hominids.

McHenry's (1973) study of the large Australopithecus humerus KNM ER 739 demonstrated that it is functionally distinct from the humeri of living hominoids but this author could not determine whether or not it was used in locomotion. Kay (1973), comparing locomotion function and body weight, concludes that the KNM ER 739 humerus was of a size to be expected if it was used for locomotion. He proposes that the robust Australopithecus was a facultative rather than habitual biped. McHenry (1973) believes, however, that Kay's estimation of body weight for this specimen is too low by some 80-100 pounds. Thus the East Rudolf specimen would then fall within the range of Homo sapiens.

Additional results on distal humeri (KNM ER 739, Kanapoi, TM 1517) were given from clustering analysis performed by McHenry (1975) which grouped the Kanapoi humerus with Homo, the specimen from Kromdraai with Pan and the specimen from East Rudolf in a unique cluster of its own but closer to Gorilla. The Kromdraai specimen in unique in its combination of wide capitulum and narrow olecronon fossa. The East Rudolf humerus, on the other hand, is like the orang in having a high capitulum but unlike Pongo in all other characteristics. This specimen is also unique in that it lacks a lateral trochlear ridge, present in all pongids studied. According to McHenry (1975), these characteristics do not yield themselves to functional explanation because the two closest related ape forms, Pongo and Gorilla, locomote in different ways. The Kanapoi fossil, dated at approximately 4.0 million years, shows the early emergence of a Homo-like elbow. McHenry (1975: 240) concludes that all three fossils may belong to separate taxa.

Further evidence of forelimb morphology was discovered by Eck in 1970 from the Shungura Formation in the lower Omo Basin. The specimen, described by Howell and Wood (1974), was a nearly complete right ulna of a robust australopithecine whose morphology shows morphological differences from modern Homo. The ulna is posteriorly convexly curved rather than sinuously curved (as seen from below) in the modern forms. This morphology is similar to that seen in living knucklewalkers. The interosseous border forms an irregular crest unlike the accentuated crest of modern ulnae, indicating perhaps significantly different patterns of stress placed on the bone. The proximal end of the anterior surface is separated by an irregular ridge of bone from the triangular-shaped area just distal to the radial notch. In contrast to prominent hollowing for the radial tuberosity in modern hominids, this rough-surfaced area is only slightly hollowed. Additionally, the length of shaft suggests elongation of the forelimb for this specimen. The combination of features are indicative of some morphological adaptations not unlike those seen in modern knucklewalkers. Additional ulnae in the sample are two proximal fragments (TM 1517, KNM ER 1500) and one complete apart from its distal end (OH 36) which shows greater curvature than the Omo specimen.

An increasing amount of evidence is suggestive that the morphology of the robust australopithecines differed significantly from that of Homo. The relative elongation and presence of specific morphological differences imply the possibility that the body of the robust forms was supported by the forelimbs, either in suspensory postures as proposed by Robinson (1972) or in terrestrial knucklewalking as proposed by Leakey (Nature (1971) 231: 241). The morphological pattern, however, is still too insufficiently defined to argue for any specific form of locomotion.

Interpretations

Precise reconstruction of the gait and stance of the earlier hominid forms is difficult, but it probably was not identical to the modern form. The same broad anatomical pattern, however, is obvious. Some anatomists such as Day (1973) are cautious in their evaluations of the anatomical differences stating that at this stage of our knowledge we do not completely understand what these differences in morphology mean in terms of locomotory function. Others such as Lovejoy (1972) and Robinson (1972) interpret these differences in terms of more specific behavioral patterns.

The study of the post crania has been hampered by poorly preserved remains and inadequately reconstructed specimens. Day (1973: 30) believes that the most complete pelvic remains from Sterkfontein (STS 14) contain major anatomical errors in reconstruction. Yet evidence (Day 1973: 42) from the available East African post cranial bones (KNM ER 803, 737) indicate clearly a bipedal gait.

According to Robinson (1972: 240-242), the capacity to stride is a complex capacity with many contributing components, the effective control of lateral balance and the extension of the femur being two of the most important considerations.

The major difference between pongid and hominid bipedal walking concerns the orientation of the ischial shaft which, in the bipedal pongid, becomes parallel to the femoral shaft and thus limits the power of the extensors of the thigh to produce a striding gait; therefore, only short steps are possible. In hominids the reorientation of the ischial shaft is directed backward and downward, in a position such that the extensors can operate to extend the thigh past the vertical position. According to Robinson the gracile australopithecine had a sufficiently well developed lumbar curvature to indicate a similar relationship with the innominate as in the modern forms, and thus this aspect of a striding gait was fully developed.

The length of the ischium has also been used to demonstrate differences between Australopithecus and modern forms. Robinson (1972: 243) claims, however, that the gracile forms had clearly shorter ischia than even the average found in modern man. Because of relatively small size of ischial tuberosity, the hamstrings could not have been large or powerful as in the Pongidae, and thus the extensor complex of the thigh was specialized for speed and for an increase in length of step perhaps even greater than in modern man.

Lovejoy (1973) provides additional information based on STS 14 which supports Robinson's diagnosis of gait of the gracile australopithecine. He outlines three principal components of a bipedal gait: 1) trunk progression and maintaining momentum, 2) trunk support and the abductor mechanism, and 3) limb progression and the pendulum gait. In each category, he claims, the joints and muscles involved were sufficiently adapted to perform in bipedal striding. In certain instances Lovejoy claims that the morphological features are indicative of more efficient locomotion. The abductor mechanism, because of the lateral iliac flare, places the origins of the abductors more lateral to the acetabulum and the longer femoral neck places the insertion more lateral to the hip joint. Lovejoy asserts (1973: 157) that this results in lesser force expended by the abductors in controlling pelvic tilt resulting in a lower pressure in the hip joint itself during locomotion. He further claims that the change from a mechanism of greater efficiency to one of lesser efficiency was the result of selection on the female pelvis to maintain adequate pelvic dimensions for an increasing fetal cranium.

Evidence for forms of locomotion in the robust australopithecines is again less complete. No direct evidence exists for the presence of the lumbar curve;

there are no known sacra. The ilium, however, was shortened and expanded posteriorly. The ischium length was relatively longer than both the gracile and the modern forms, but because the robust ilium was similar to the gracile counterpart it would seem unlikely that the limb extensor mechanism would be identical to that of modern pongids.

Robinson concludes that the robust condition was a compromise between the quadrupedal arboreal climbing pattern of the African apes and efficient bipedalism, implying a combined bipedality with some locomotor activity that required power in the use of the limb extensor mechanism.

CATALOGUE OF FOSSIL HOMINID POST CRANIA

	SPECIMEN #	SITE LOCATION	DESCRIPTION
HAND	18-1848 (1970)	Loc Omo 18	left middle phalanx
	OH 18	FLK Olduvai	phalanx
	KNM ER 164	Ileret Area 104	right(?) three phalanges, metacarpal
	TM 1526	Sterkfontein lower breccia	capitate
	TM 1517	Kromdraai	left metacarpal II
	TM 1517	Kromdraai	proximal phalanx
RADIUS	75-S-1 317 (1970)	Loc Omo 75-S	proximal end
	OH 49	FLKNN	shaft
	MLD 15	Makapansgat	right distal end
	MLD 16	Makapansgat	right proximal end
	MLD 32	Makapansgat	left proximal end
	STS 68	Sterkfontein lower breccia	proximal end
	SK 18	Swartkrans pink breccia	proximal end
ULNA	40-19	Loc 40 (Omo)	right ulna
	TM 1517	Kromdraai	right proximal end
	KNM ER 803	Ileret	fragment
	KNM ER 1500	Ileret	proximal fragment
	OH 36	SC	complete except for distal end
HUMERUS	OH 13	MNK II (Olduvai)	distal humeral shaft
	KNM ER 739	Ileret	right distal end and shaft

	SPECIMEN #	SITE LOCATION	DESCRIPTION
	KNM ER 740	Ileret	left fragment of distal end
	Kanapoi Hominid 1		left distal end
	MLD 14	Makapansgat	distal right fragment of shaft
	MLD 39	Makapansgat	right distal fragment
	STS 7	Sterkfontein	proximal fragment
	STS 50	Sterkfontein	right distal end
	SK 860	Swartkrans	distal end
	TM 1517	Kromdraai	right distal end
SCAPULA	STS 7	Sterkfontein lower breccia	fragmentary
CLAVICLE	OH 48	FLKNN I	clavicle
	MLD 20	Makapansgat	right acromial extremity
	MLD 36	Makapansgat	left acromial extremity
RIBS	OH 50	FLK NN (Olduvai)	rib shaft
VERTEBRA	105-7	Loc 105 (Omo)	lumbar
	KNM ER 164	Area 104	seventh cervical, first thoracic
	STS 14	Sterkfontein Lower Breccia	9 thoracic, all lumbar, sacrum
	STS 65	Sterkfontein Lower Breccia	vertebral centrum
	SE 2398	Sterkfontein Middle Breccia	vertebra
	SK 853	Swartkrans	lumbar vertebra
	SK 854	Swartkrans	axis
	SK 3981a	Swartkrans	last thoracic
	SK 3981b	Swartkrans	last lumbar

	SPECIMEN #	SITE LOCATION	DESXRIPTION
PELVIS	SK 3155b	Swartkrans	adolescent nearly complete ilium, parts of ischium, pubis
	SK 1590d	Swartkrans	innominate parts
	MLD 7	Makapansgat	left adolescent ilium
	MLD 8	Makapansgat	right adolescent ischium
	MLD 25	Makapansgat	left adolescent ilium
	MLD 21	Makapansgat	fragmentary ilium
	MLD 35	Makapansgat	fragmentary infant ilium
	STS 14	Sterkfontein Lower Breccia	left and right innominates
	STS 65	Sterkfontein Lower Breccia	1/10 pubic fragment
	SK 50	Swartkrans	right innominate lacking iliac crest
	TM 1605	Kromdraai	ilium lacking iliac crest
FEMUR	754-8	Loc 754 (Omo)	portion femoral drophysis
	OH 20	HWK II (Olduvai)	left proximal shaft and neck
	KNM ER 736	Koobi Fora	left femoral shaft
	KNM ER 738	Koobi Fora	left shaft and proximal end
	KNM ER 737	Koobi Fora	left femoral shaft
	KNM ER 999	Ileret	left femur lacking lateral condyle
	KNM ER 815	Ileret	left femur without head
	KNM ER 993	Ileret	right femur
	KNM ER 1481	KF Karari Escarpment	left femur
	KNM ER 1472	KF Karari Escarpment	right femur
	KNM ER 1475	KF Karari Escarpment	right proximal end and shaft

	SPECIMEN #	SITE LOCATION	DESCRIPTION
	KNM ER 1807	Area 103	right femur shaft
	KNM ER 1809	Area 127	right femur shaft
	L-129-3	Loc AL 129 (Afar)	right proximal end
	L-128-1	Loc AL 128	proximal left end
	L-129-1	Loc AL 129	distal right end
	MLD 17	Makapansgat	femoral head
	TM 1513	Kromdraai	left distal end
	STS 14	Sterkfontein Lower Breccia	proximal end
	STS 34	Sterkfontein Lower Breccia	right distal end
	STS 65	Sterkfontein Lower Breccia	left proximal femur
	SK 82	Swartkrans	right proximal femur
	SK 97	Swartkrans	right proximal femur
	SK 1590d	Swartkrans	head of proximal end
	TM 3601	Kromdraai	distal end femoral condyle
	KNM ER 803	Lake Rudolf	left shaft
TIBIA	OH 35	FLK	left shaft and distal end
	KNM ER 741	Ileret	left proximal end and shaft
	KNM ER 813	Koobi Fora	fragmentary tibia
	KNM ER 1481	KF Karari Escarpment	distal end
	KNM ER 1810	Area 123	left proximal portion
	L-129-2	AL 129 (Afar)	right proximal end
	KNM ER 803	Ileret	left shaft
FIBULA	KNM ER 1481	KF Karari Escarpment	distal portion
	KNM ER 803	Ileret	fragment of shaft and distal end

	SPECIMEN #	SITE LOCATION	DESCRIPTION
FOOT	576-18	Loc 576 (Omo)	right? distal phalanx hallux
	OH 8	FLK NN I (Olduvai)	left 7 tarsals, 5 metatarsals
	KNM ER 997	Koobi Fora	proximal metatarsal
	KNM ER 813	Koobi Fora	right talus
	KNM ER 1815	Ileret	right talus
	TM 1517	Kromdraai	right talus, proximal and distal phalanx
	OH 43	Olduvai	metatarsals
	KNM ER 803	Ileret	talus, third left metatarsal, phalanges

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ENDOCRANIAL VOLUME IN PLIO/PLEISTOCENE HOMINIDAE

Endocranial volume of fossil hominids has been used by many workers to demonstrate whether or not a particular specimen has reached a specific level of development. The fact that natural selection kept favoring larger brains throughout the Pleistocene has been well demonstrated. Yet as Holloway (1966: 115) suggests, there has been no firm connection made between the neural structures of the cortex and the increasing behavioral complexity upon which natural selection was operating. In other words, endocranial volume which increased during the Pleistocene period has not been related to absolute or relative differences in cultural capabilities. Keeping in mind that the range of variability in modern *Homo sapiens* is nearly 1000 cc without measurable behavioral differences between the extremes of the range (Van Valen 1974). Holloway suggests that other parameters, besides absolute volume, must be used to explain the increase in cranial capacity in the course of hominid evolution.

According to Holloway (1966: 117), however, neural organization during the australopithecine stage resulted in a shift into essentially human behavior and the continuing changes resulted in greater degrees of behavioral complexities rather than kinds.

Attempts at understanding hominid evolution through increased cranial capacity is grossly oversimplifying the problem. Yet Jerison (1963) has shown that though certain limitations on understanding exists in the study of fossil endocasts, specific information not only as to (1) total volume, but also (2) linear measurements producing indices of size, (3) proportional measures of surface areas, and (4) the diameters of nerve bundles as estimated from the cranial foramina can be obtained. Despite the valid criticisms most judgments concerning the evolution of the human brain use brain volume as the main quantitative basis, and Jerison (1963: 268) points out that large random errors approaching 20 percent exist in volume measures because only rarely is a natural endocast recovered from a deposit in perfect condition.

Earliest estimates (Broom and Robinson 1948, Ashton 1951) of existing fossil hominids yielded figures of 415 cc (STS 5), 450 cc (TM 1511), and 650 cc (TM 1517, the type specimen Paranthropus robustus from Kromdraai). It was believed that the males had substantially larger brains than the females based on the single large mandible (STS 7) which Broom and Robinson estimated must have supported a skull with an endocranial volume of "well over 700 cc and perhaps more than 750 cc." The primary purpose of these early works was to demonstrate the human qualities of the fossil forms. Thus Broom and Robinson state that "if Plesianthropus was not quite human, it was nearly human."

By the 1960's the idea of the cerebral "rubicon" of brain size differentiating man and apes formulated by Keith, Vallos and others was replaced by the knowledge previously stated that brain volume has little relationship to functional behavioral capabilities. Because of interest in cranial capacities from the point of view of determining where the australopithecines fit in relation to other hominoids, Tobias (1963, 1971) reviewed the estimates for cranial capacity in the known australopithecine and modern hominoid forms. Until the discovery of the OH 5, it had generally been considered that the robust australopithecines had larger brains than the gracile forms and estimates of cranial capacity varied between 650 cc and 1000 cc. The well-preserved skull OH 5 type specimen of Zinjanthropus boisei was the first of the robust australopithecines to enable an accurate assessment of cranial capacity. Tobias (1971) gives an estimate for this specimen at 530 cc and in addition for SK 1585 at 500 cc. Holloway's (1970, 1972) estimate for the same specimen (SK 1585) is 530 cc. More recently, Holloway (1973) has calculated the endocranial volume of two robust specimens from East Lake Rudolf, KNM ER 406 and 732, which yielded figures of 510 and 506 cc respectively.

For the gracile australopithecine Tobias (1971) reports on Taung (540 cc), STS 60 (435 cc), STS 5 (480 cc), STS 71 (480-520 cc), STS 19/58 (530 cc) and MLD 37/38 (480 cc) and establishes a mean endocranial volume at 494 cc, and a total range for adult australopithecines including the two robust forms at between 435-540 cc. This compares with a similar estimate by Holloway (1970) of the australopithecine range between 428-530 cc. This differs from estimates given by Wolpoff (1969) of a mean value of 521 cc and a range between 435-657 cc which includes Olduvai Hominid 7. Tobias (1971: 27) demonstrates that an estimate can be made of the projected australopithecine population range based on the sample mean ± 3 standard deviations which gives the values of 370-618 cc. The estimated population range is consistent with that reported by Zuckerman (1928) for chimpanzees (290-500 cc) and by Schultz (1965) for pygmy chimpanzees (275-380 cc). It is not consistent with estimates of 1000 cc for the maximum limits of the australopithecine cranial capacity (Broom and Robinson 1952, Dart 1956).

Endocranial volume enters into the issue of the status of many individual fossils, the most notable being Olduvai Hominid 7 designated the type specimen of Homo habilis Leakey. Tobias (1964, 1965) estimated the range of possible values for this juvenile specimen which varied from 643-724 cc, with a mean of 680 cc which exceeds the mean for the australopithecines by slightly more than 3 standard deviations (Tobias 1965, 1968). Tobias' estimate of the mean of OH 7 has been confirmed by Holloway (1965) but revised by Tobias (1968) to 657 cc. The question of whether or not this difference was of taxonomic significance was argued by Holloway and Tobias (1966), Tobias claiming that our knowledge of australopithecine variability was insufficient to suggest whether or not these hominids were highly variable in cranial capacity comparable to Gorilla with a high coefficient of variability (13.6) or comparable to Pan with a low coefficient of variation (6.8). Wolpoff (1969, 1970), however, claims that his estimate of the australopithecine mean (521 cc) justifies the inclusion of OH 7 within his taxon Homo africanus. Pilbeam (1969, 1970) criticizes this methodology and claims that

Wolpoff's "sample" is not drawn from a single population in time or space and, therefore, it is unwise to draw any taxonomic conclusions.

Holloway (1970a, 1970b), however, argues that, based on his more recent australopithecine estimates which give a mean of 464 cc (which includes two robust forms OH 5, SK 1585), contentions that the robust and gracile forms were male and female of the same species is highly unlikely as is the contention by Wolpoff (1969) that OH 7 should be included taxonomically with the australopithecines from South Africa. Similar arguments were proposed for the inclusion of OH 13, 24 within the genus Homo rather than Australopithecus (Tobias 1972, Holloway 1973), whose estimates of cranial capacity approached 650 cc and 590 cc respectively.

The question of the affinities of the Taung skull has remained open because of the young age of this specimen and the difficulty in estimating what additional development this individual would have made if it had lived to reach adulthood. Ashton and Spence (1958), by determining the dental age of the Taung child, determined that the cranial capacity had reached 90 to 94 percent of its adult values. This established the "adult value" at 562 cc replacing earlier estimates of 600 cc. More recent reconstructions of the Taung endocast (Holloway 1970) produced significantly different results which averaged 440 cc. If the Taung child is indeed a late robust australopithecine, the estimate for endocranial volume is considerably lower than those of adult individuals of the same period.

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E. Problems in Interpretation: The Taxonomy of Early Hominidae

TAXONOMY OF THE FOSSIL HOMINIDS
OF
SOUTH AFRICA

The result of paleontological explorations in South Africa brought to light at least two distinct forms of fossil hominid recognized in the faunal remains. Robinson ('63) and earlier ('54) established generic distinctions between two of the forms of hominids commonly known as the gracile and robust form of Austrolopithecine. Taxonomic distinctiveness was supported on the one hand by morphological differences between the two fossil forms and on the other hand by ecological differences which were based primarily on diet. Brain's (58) original work on the climatic sequence of the South African cave sites suggested that those cave occupied by the robust forms were found during wetter phases, periods of heavier rainfall, and that the caves occupied by the gracile forms were during periods of less rainfall. The diet of the robust form was proposed to be primarily vegetarian. Brain's work was criticized by Vrba ('75) whose investigations suggested a more dry period for the accumulation of the deposits of the robust austrolopithecine bearing caves. Thus, the argument is whether the robust forms were eating vegetable matter in a wetter and more luxuriant environment, or one of more drier conditions, in which case, Jolly's ('70) argument for "small object" feeding on tough grassland vegetable material is more appropriate.

The morphological differences in the two forms are primarily found in the dentition and skull. According to Robinson ('63) the morphology of the first lower deciduous molar (dm_1), the shape of the permanent lower canine, the proportion of the anterior and posterior teeth, shape of the palate, the shape and structure of the face and of the braincase are all approximate diagnostic characters to justify separation of the two hominids into two distinct genera: Paranthropus which is represented at Swartkrans and Kromdraai and Australopithecus which is represented at Sterkfontein (= Plesianthropus) and Makapansgat. Robinson retained the subfamilial rank, Australopithecinae, to accommodate these two genera. Dart, however, since 1948 has held the view that the whole Australopithecine group represented a single genus with two species within the family Hominidae. This view has been supported by Washburn and Patterson (1951), Oakley (1954, 1956), LeGros Clark (1964, 1967) and Leakey, Tobias and Napier (1964). Tobias (1968) proposed that three species be recognized under the single genus, namely A. africanus, A. robustus and A. Bosei (Olduvai Hominid^5) and provided diagnosis for each.

Recent attempts to sink the genus Australopithecus had their origins with Mayr ('50) who proposed a classification of the australopithecines as distinct species of the genus Homo, specifically Homo transvaalensis. He subsequently abandoned this view ('63).

The arguments for a single hominid genus leading to modern man was revived from two points of view. One by Robinson ('72: 1-11) who includes the genus Australopithecus (but not Paranthropus) in the same phyletic line as Homo. He claims that because Australopithecus represents an early phase in the establishment of the adaptive pattern characteristic of modern man that it would be logical to sink the *Australopithecus* into the genus *Homo* as a junior synonym. Thus, his most recent classification of known Plio-Pleistocene hominids includes only two genera *Paranthropus* and *Homo*. After lengthy justification, Robinson concludes that the appropriate specific name for those specimens of the gracile australopithecine group is *Homo africanus*.

The second point of view was first proposed by Wolpoff ('68, '71) whose extreme lumping of both the robust and gracile australopithecines into a single species has not met with general acceptance. The basis for the single species hypothesis is the nature of the primary hominid adaptation which Wolpoff claims is culture or structured learned behavior. Wolpoff ('71: 607) argues that in order for closely related species to coexist sympatrically "they must differ from each other in such a manner that they do not enter into a 'struggle for existence' in which one succeeds at the expense of the other." He concludes that for culture-bearing hominids this would be a particularly difficult thing to avoid.

Wolpoff ('73) redefends his position claiming that the criteria which are used to separate the South African australopithecines into two taxa are either unverifiable or related to general body size differences. Recently Wolpoff and Lovejoy ('75) rediagnosed the genus *Australopithecus* with the single species, *africanus*, and incorporates as junior synonyons all members of the general *Paranthropus*, *Paraustralopithecus*, *Plesianthropus*,*Zinjanthropus*, *Meganthropus africanus*, *Homo habilis* and *Telanthropus*. These authors suggest that the taxon *Australopithecus* should be retained and not sunk into the genus Homo. They argue that the discovery of additional specimens occupying the same adaptive plateau as the known australopithecine will certainly increase the knowledge of the amount of morphological variability used to define the genus and thus approach the larger range of variation used to define the genus Homo.

The taxonomic position of the hominid specimens from Swartkrans originally described as Telanthropus capensis Broom, 1950 has been one considerable debate. Consisting originally of a mandible (SK 15) and later a right mandibular fragment (SK 45), maxillary fragment (SK 80) and finally a facial part of a cranium (SK 847) and associated temporal fragment SK 8466 (the latter three belonging to the same individual, Clarke and Howell, '72) it was first described as an early type of man morphologically distinct from the australopithecines. Dart ('55) believed it represented a female robust australopithecine. Pilbeam ('70) thought it was a gracile australopithecine, though he later ('72) revised this view. Howell ('67) on the other hand, was of the opinion that the specimens belonged to the taxon Homo erectus. This argument followed Robinson's ('61) formal sinking of the genus Telanthropus into Homo, and Tobias and Von Keonigsvold's ('64) demonstration of the similarity of SK 15 with the Homo erectus mandible (Sangiran B) from Java, and Olduvai Hominoid 13 (= Homo habilis). Wolpoff ('68, '71) attempted to claim, however, that no morphological evidence validly distinguished these specimens from the other australopithecines, rather he thought that "Telanthropus" representedan extension of the estimated australopithecine range of variation. This position was carefully reviewed and criticized by Clarke and Howell ('72) and Gutgesell ('70) who reviewed the diagnostic characteristics which were used to place the composite SK 847 within the genus Homo. Clarke and Howell ('72) refrained from placing the "Telanthropus" in the Homo erectus group because they suspected that the remains might prove to be conspecific with Homo habilis from Olduvai. The recent age determinations for the South African fossiliferous localities create certain new taxonomic problems. The placement of the Makapansgat deposit at the oldest end of the sequence appears, on the one hand, seems to be consistent with the evidence of the hominid fossils themselves. In Tobias' view ('73: 80-81) the Makapansgat hominids are characterized by traits which include some robust features in crania, jaws and teeth. Tobias ('69) speculated that perhaps more than one species of hominid was represented in the assemblage. Aguirre ('70) further claimed that the Makapansgat juvenile jaw, MLD2, represented an adolescent A. robustus. More recently, Tobias ('73) revised his opinion and pointed out that in an early population of A. africanus which was close to the point of speciation into robust and gracile forms that intermediate characteristics might well be expected and that the Makapansgat hominids might be looked at as basal stem stock.

The idea that A. africanus gave rise to two hominid lineages, one giving rise to the robust form and the other leading to the genus Homo has been criticized by Robinson ('72: 4-5) who suggested the possibility that the origin of the Paranthropus line extends back into the early

Pliocene to fossils similar to those recovered by Simons and Chopra ('69) in India and attributable to the taxon Gigantopithecus bilaspurensis.

The recognition that the original australopithecine site at Taungs was much younger than previously believed also had taxonomic implications. On the basis of these age estimates the Taung adolescent lived some 2 m.y. after those at Makapansgat or Sterkfontein. As far as the evidence presently shows during the intervening time period, only early specimens of the genus Homo or A. robustus were present. In light of this, Tobias questions whether the Taung specimen in fact represents A. africanus as defined by the Sterkfontein and Makapansgat remains. Because of the small brain and dental characteristics it is excluded from the category Homo erectus. It may ultimately prove to be a late surviving member of A. robustus approximately contemporary with the East African forms from Chesowanja. According to Tobias (73: 82) if the Taung skull is removed as the type specimen of A. africanus under the rules of zoological nomenclature it may be assigned a position of lectotype of A. robustus. However arguments could be made because of priority to designate the Taung skull as the type specimen of A. robustus. If this occurred, the robust australopithecines would be placed in the taxon A. africanus which would make this taxon unavailable for use for the gracile form. This event would leave the question of what to call the gracile australopithecines open to further debate (see Olson, 1974).

TAXONOMY OF EAST AFRICAN HOMINIDS

The discovery of Olduvai Hominid 5 from FLK I began an intensive search for early man in East Africa. The problems involving the taxonomy and relationships between the newly discovered fossils were fewer primarily because paleoanthropologists by this time had, for the most part, ceased regarding every new fossil hominid as a new species. Added to this was the trend in zoological nomenclature to expand the concept of variability in dealing with paleospecies which made it more likely that divergent specimens would be grouped within the same taxon.

The majority of problems in the literature arise in the description of fossil specimens from Olduvai Gorge. As early as 1959 Leakey described Olduvai Hominid 5 as a member of the sub-family Australopithecinae which, in certain respects, recalled the genus Paranthropus, but he believed that the new specimen differed from both Australopithecus and Paranthropus more than those two genera differed from each other. As a consequence he created a new genus and species, Zinjanthropus boisei, and proposed a preliminary diagnosis (1959: 492-493) of the new taxon.

Robinson (1960) took issue with Leakey's description claiming that most of the differences Leakey proposed were the result of size. Zinjanthropus was somewhat larger and more muscular than the known South African forms. The other features of the new East African hominid, Robinson claimed, could also be demonstrated in the robust South African forms.

In 1961(a, b) Leakey announced the discovery of yet another specimen from the site of FLK NNI, a horizon claimed to be older than that of Zinjanthropus. This specimen OH 7 consisted of a nearly complete mandible associated with stone and bone tools. Leakey believed that it represented not an australopithecine but a primitive ancestor of the genus Homo. In 1964 Leakey, Tobias and Napier revised the diagnosis for the genus *Homo* and include a new species which they named *H. habilis*, the species name suggested by Raymond Dart.

The type specimen of *Homo habilis* included the original mandible of OH 7 from Bed I. The paratypes included an incomplete cranium (OH 13) from MNK II, Bed II, associated post crania (OH 8) from FLK NNI, teeth and cranial fragments (OH 6) from FLK I, and a mandibular fragment (OH 4) from MNK I. Referred material included additional cranial fragments (OH 14) from MNK II, and a fragmentary skull with dentition (OH 16) from FLK II, Maiko Gully. Leakey subsequently placed OH 16 in the lineage leading to *Homo erectus* as represented by the skull from site LLK II. Mary Leakey (1969, 1971) provided additional referred material to *Homo habilis* including OH 24, a nearly complete cranium from Lower Bed I, site DK East, and OH 21, OH 27, isolated teeth from Bed I, FLK North and HWK East, respectively. M. Leakey (1971) (contra L. Leakey) includes OH 16 with the type specimen as part of the *habilis* group which represented males. Accounting for the differences by sexual dimorphism between these specimens and OH 13 and OH 24, M. Leakey refers to the latter specimens as females. The major importance of the discoveries at Olduvai was that it demonstrated conclusively that at least two forms of hominids were coeval.

Taxonomic questions arose (Oakley and Campbell 1964) over the relationship between *Homo habilis* and the South African form *Telanthropus capensis*, which had already been referred to as *Homo erectus* by Robinson (1961). These authors claimed that if *Homo habilis* proved to be conspecific with *T. capensis*, the name *capensis* would have priority over that of *habilis* but only for the genus *Australopithecus* as *capensis* was already occupied in the genus *Homo* through the actions of Broom (1917) in describing a skull from Boskop, South Africa.

The relationship between *Homo habilis* and earlier and later forms was suggested by Montagu and Tobias (1965). Tobias was of the opinion that *H. habilis* stood intermediate in position between *Australopithecus* and *Homo erectus*, and believed that the interim solution of describing the specimen as a "lowly species of Homo seems a reasonable compromise." Montagu, on the other hand, thought that Homo habilis could perhaps be more appropriately regarded as an early form of Homo erectus. Tobias (1966a, b) and Leakey (1966, 1969) reargued this position ans Tobias (1966b: 957) concluded that perhaps the more correct taxonomic label would be Homo erectus habilis. Leakey (1966: 1280), however, disagreed with Tobias in that H. habilis represented a stage in evolution from A. africanus to H. erectus, rather it seemed to him that H. habilis and H. erectus, as well as certain australopithecines, all represented distinct lineages by the early Pleistocene. Homo erectus, he believed, became extinct while Homo habilis subsequently gave rise to Homo sapiens.

Robinson (1966) again strongly disagreed claiming that the proponents of Homo habilis failed to treat variability in fossil forms adequately or realisticall and that the criteria which were used to sort Homo habilis from Australopithecus were not valid. His position was defended by Bielicki (1966), Brace (1968), and Simons, Pilbeam and Ettel (1969). The primary criticisms for Homo habilis given by Simons et. al. (1969: 252-259) were that the Bed I material closely resembled Australopithecus sp. from South Africa and that the evidence suggested that Bed I Homo habilis should be grouped with A. africanus. The Bed II material, however, differs from Bed I material in size and morphological detail and resembled Homo erectus in certain morphological details. Additionally the material from these two deposits represent distinct temporal spans separate from one another by as much as a million years.

The problems involving the taxonomy from the remainder of the East African sites yielding fossil hominids has almost entirely been avoided due to the cautiousness of researchers in proposing new names. With two exceptions, the fossil hominids recovered from the deposits of Lake Rudolf and elsewhere have been grouped wither within the genus Homo or within the genus Australopithecus.

Arambourg and Coppens (1967) provisionally describe a mandible from the lower Omo Basin as Paraustralopithecus aethiopicus and Coppens (1965) suggested that a cranio-facial fragment from Chad which appeared similar to Homo habilis should be referred to as Tchadanthropus uxoris. Both names have not been well accepted by other investigators and may be considered obsolete.

The material from East Lake Rudolf was from its earliest descriptions referred to the australopithecines with the exception of scattered occurrences of what R. Leakey (1971) described as members of the genus Homo in which he placed KNM ER 730, 731 and 737. He argued that the concept of the gracile australopithecine being ancestral to Homo would require reexamination and suggested , following Wolpoff and Brace, that the gracile variety may prove to be the female of the robust form. More recently R. Leakey has added to the list of members of the genus Homo, which include KNM ER 164, 803-809, 811, 813, 817, 820, 992, 1462, 1466, 1470, 1472, 1475, 1480, 1481, 1483, 1501, 1502, 1507, 1508, 1510, 1590, 1591, 1593, and 1800-1820. R. Leakey (1973) professed doubt concerning the taxonomic status of the material. The most complete cranium KNM ER 1470 was claimed to be quite distinctive from Homo erectus in the form of the facial and maxilla regions. He also did not wish to attribute specimen 1470 to the taxon H. habilis primarily because his specimen was larger brained and from a supposedly earlier time period. R. Leakey (1974), however, in his study of the 1973 collection including KNM ER 1802 and 1813, claimed that these specimens may demonstrate the presence of a third hominid lineage who possessed hominine dentition but whose cranial capacity appeared small. He compared these specimens with OH 24 of similar dentition and cranial capacity, and also with material from Sterkfontein. Additionally he proposed a fourth line which he believed to be remnant of earlier populations to include the Omo mandible described as Paraustralopithecus and KNM ER 1482.

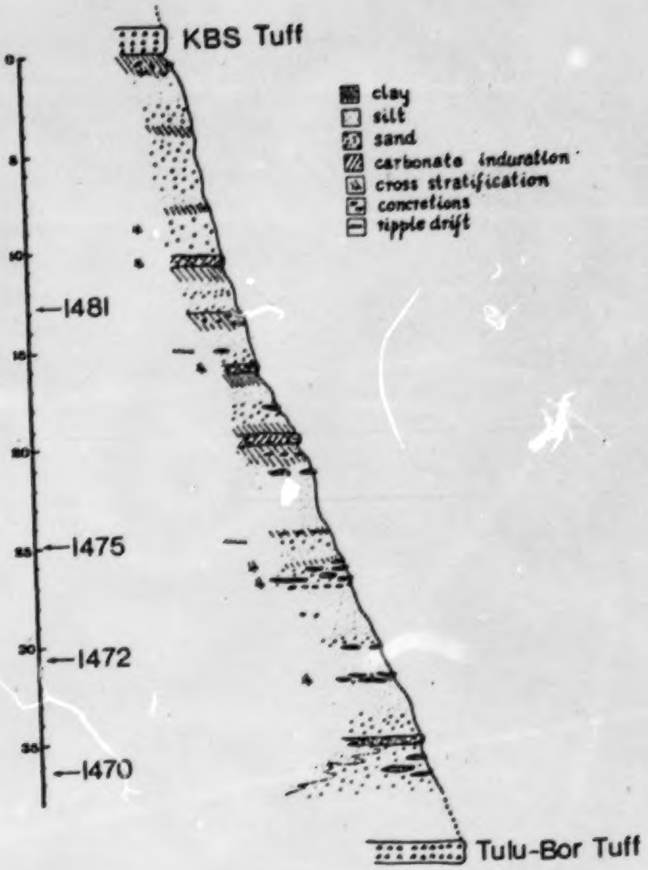
Robinson (1972), claiming that Leakey had used the diagnostic features of Paranthropus as a working definition of "australopithecine" as a whole, questioned whether the known sample of hominids from East Rudolf are basically the same as the sample from South Africa. He believed that morphologically and adaptively the robust australopithecines in the two regions represent members of the same lineage, and that the smaller hominids, Leakey's Homo sp. and Robinson's Homo africanus, were also basically of the same stock.

More recently Campbell (1973) has proposed a revised taxonomy for fossil man in which he establishes two species of Australopithecus—a large form, boisei, and the more gracile form, africanus. From the evidence of the post crania he claimed that both forms were bipedal and savannah adapted, but must have originally been geographically isolated to permit speciation. He believed that A. boisei could have occupied savannah regions of southern Eurasia, thereby competing with Gigantopithecus, and then secondarily occupied the grasslands in Africa.

Campbell revises the status of the South African hominids by claiming that few meaningful distinctions can be made between the robust and gracile specimens and that both forms are actually represented in all deposits except Taung. For this reason he lumps all of the South African fossils into one category, Australopithecus africanus. Included also in this category is Homo habilis from Olduvai and KNM ER 1470 from East Rudolf.

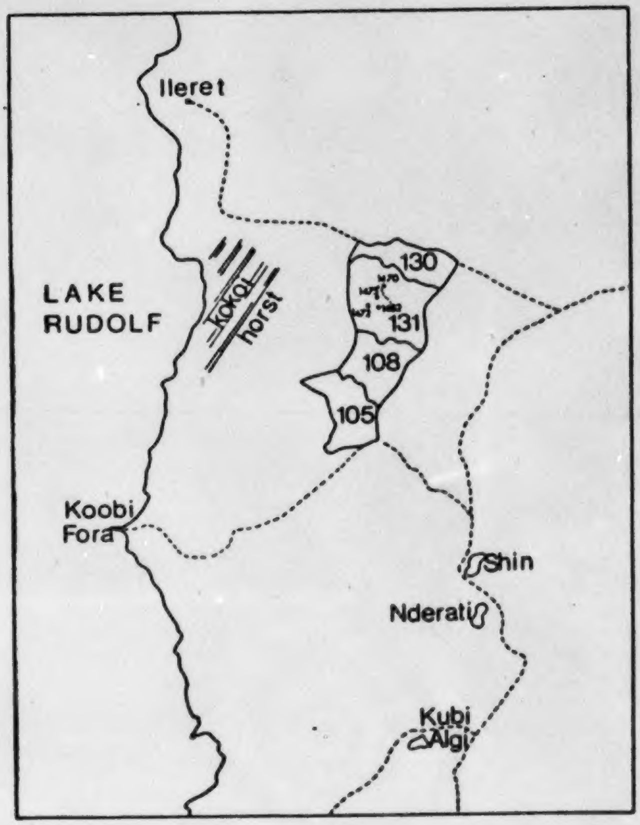
Campbell asserts that taxonomy should be based on chronology, that Australopithecus should be retained as a taxonomic label for the early members of the lineage leading to modern forms. This genus was succeeded by the genus Homo in time at approximately 1.5-1.3 million years. Generic distinction between the two forms is based, in his words, on "a whole series of related cultural developments based on language and technology which enabled the hominids to adapt to and survive in zones of low climatic equability" (Campbell 1973: 200).

Figure II - 33


KBS Tuff
clay
silt
sand
carbonate induration
cross stratification
concretions
ripple drift
0
5
10
15
20
25
30
35
1481
1475
1472
1470
Tulu-Bor Tuff

Stratigraphical successions of the deposits in Area 131 yielding hominids 1470, 1472, 1475 and 1481. Relationships to the KBS Tuff.
(From Leakey (1973):440)

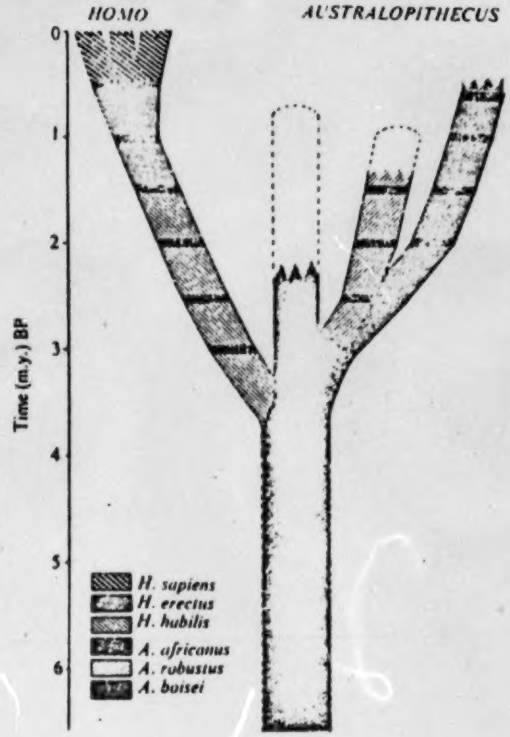
Figure II - 34


Ileret
LAKE RUDOLF
kokoi
horst
130
1470
131
108
105
Koobi Fora
Shin
Nderati
Kubi Algi

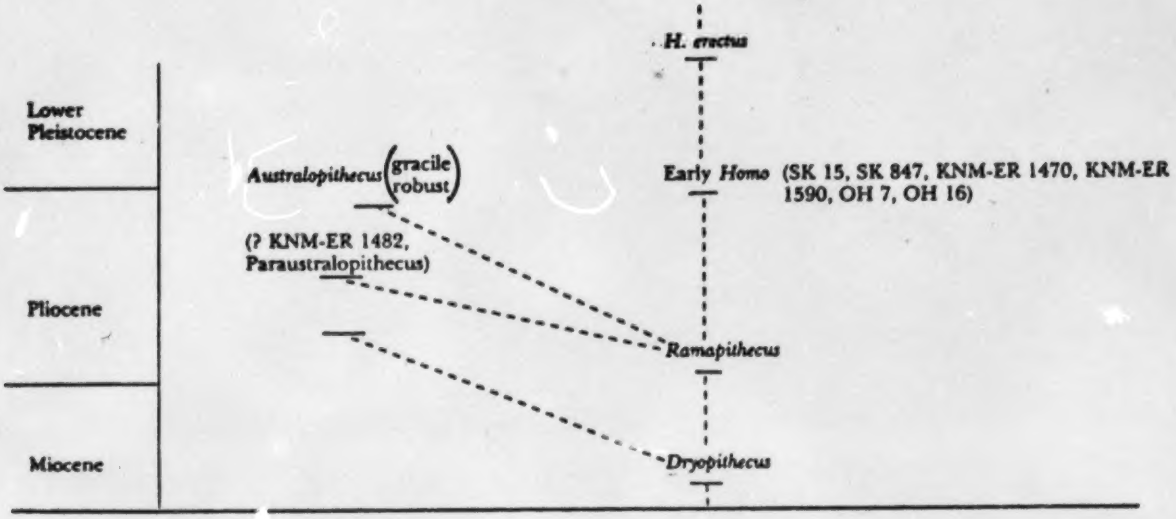
Distribution of sites of fossil hominids KNM ER 1470, 1472, 1475 and 1481 in the East Rudolf, Kenya.
(From Leakey (1973):448)

PROVISIONAL PHYLOGENETIC TREES OF PLIO-PLEISTOCENE HOMINIDAE

Figure II - 35

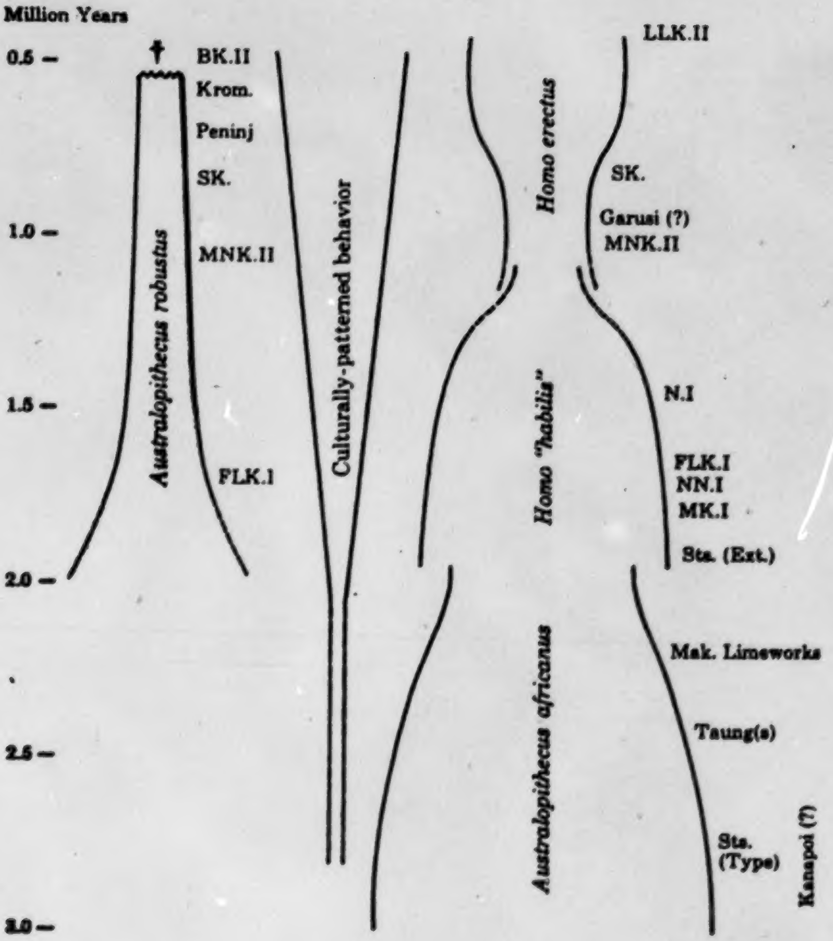

HOMO
AUSTRALOPITHECUS
Time (m.y.) BP
0
1
2
3
4
5
6
H. sapiens
H. erectus
H. habilis
A. africanus
A. robustus
A. boisei

From Tobias, Nature (1973) 246: 82.


H. erectus
Lower Pleistocene
Pliocene
Miocene
Australopithecus (gracile robust)
Early Homo (SK 15, SK 847, KNM-ER 1470, KNM-ER 1590, OH 7, OH 16)
(? KNM-ER 1482, Paraustralopithecus)
Ramapithecus
Dryopithecus

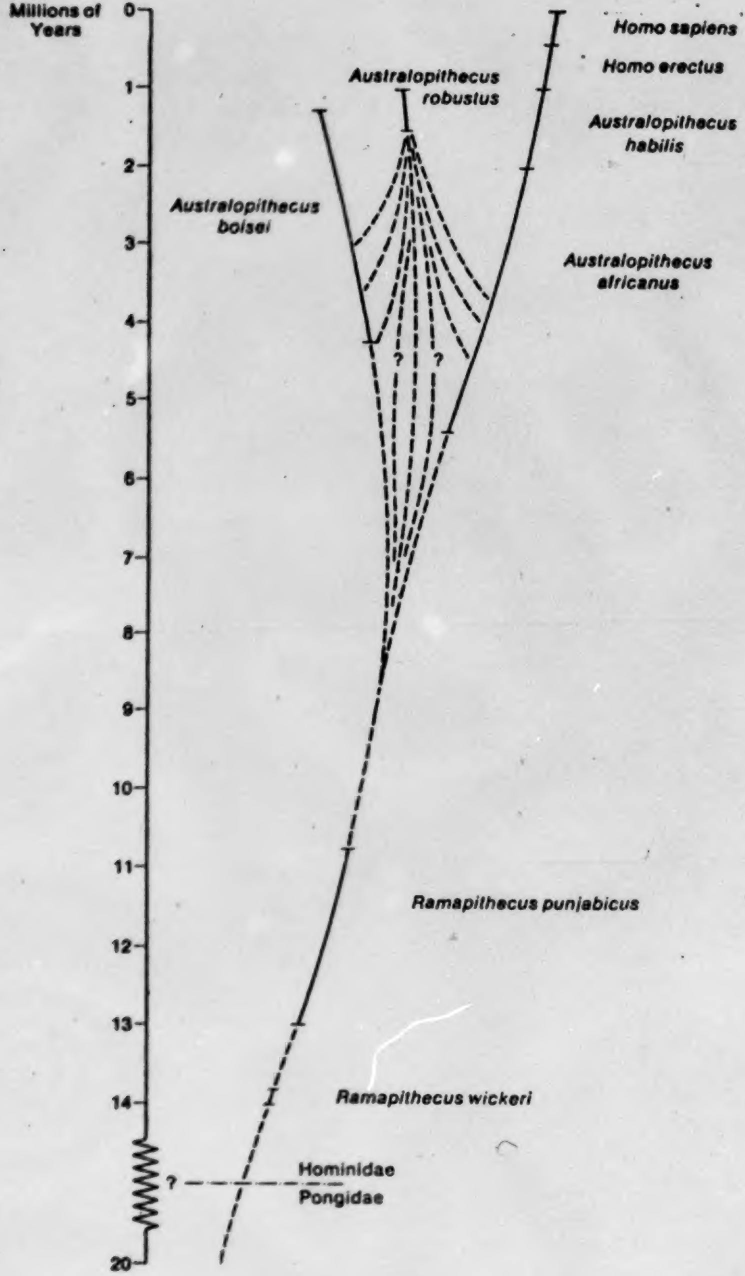
From Butzer, Current Anthropology (1974) 15: 419.

Figure II - 36



LeGros Clark. In Howell, American Journal of Physical Anthropology (1967) 27: 100.

Figure II - 37


Millions of Years
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
20
Homo sapiens
Homo erectus
Australopithecus robustus
Australopithecus habilis
Australopithecus boisei
Australopithecus africanus
?
?
Ramapithecus punjabicus
Ramapithecus wickeri
?
Hominidae
Pongidae

From Pilbeam (1972), The Ascent of Man: 13.

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Simons, E. and S. Chopra
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Simons, E., D. Pilbeam and P. Ettel
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1968 The taxonomy and phylogeny of the australopithecines. *In* Taxonomy and Phylogeny of Old World Primates with Reference to the Origin of Man, B. Chiarell, ed.

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Wallace, J. A.
1973 Tooth chipping in the australopithecines. Nature 244: 117-118.

Washburn, S. and B. Patterson
1951 Evolutionary importance of the South African "man-apes". Nature 167: 650-651.

Wolpoff, M. H.
1968 "Telanthropus" and the single species hypothesis. American Anthropologist 70: 477-493.

1969 Facts and theories in the taxonomy of *Paranthropus* and *Australopithecus* (*Homo*). American Journal of Physical Anthropology 31: 256.

1970 The evidence for multiple hominid taxa at Swartkrans. American Anthropologist 72: 576-607.

1971a Competitive exclusion among lower Pleistocene hominids: the single species hypothesis. Man 6: 601-614.

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Wolpoff, M. H. and O. Lovejoy
1975 A rediagnosis of the genus *Australopithecus*. Journal of Human Evolution 4: 275-276.

F. Bibliography of Miocene Hominoids

BIBLIOGRAPHY OF MIOCENE HOMINOIDS

Andrews, Peter

1971 *Ramapithecus wickeri* mandible from Fort Ternan, Kenya. Nature 231: 192-194.

> Describes the specimem (KNM FT 45) from Fort Ternan consisting of a portion of the left corpus of the mandible complete nearly to the midline of the symphysis, with crowns of both premolars. The body and symphyseal region is relatively low and robust. The morphology of the zygomatic process, maxilla and dentition suggest adaptation for powerful lateral grinding and claims that the East African and Indian forms of Ramapithecus are at least specifically distinct.

1974 New species of *Dryopithecus* from Kenya. Nature 249: 188-190.

> Abstract: Two new species of Pongidae, assigned to a new subgenus of Dryopithecus, are described. These assignations are based mainly on new specimens discovered recently in Kenya, but some other specimens are reassigned to the hypodigms of the new species. A more complete revision of the African early Miocene dryopithecines is in preparation. Photographs of the upper dentition of several species of dryopithecines and new mandible of *D. gordoni* are included as plates. Measurements of M^1 of *D. gordoni* and *D. vancouveringi* are included.

Conroy, G. C.

1972 Problems in the interpretation of *Ramapithecus* with special reference to anterior tooth reduction. American Journal of Physical Anthropology 37: 41-47.

> Tabulates 16 facial and dental characteristics which can be used to describe the hominid affitinities of the *Ramapithecus* material. Defines relative anterior dental reduction as referring to the overall incisor size (area) as compared to an $M^1 + M^2$ area which he claims is reduced from *Ramapithecus* to *Homo* but is increased from *D. africanus* to *Pan*. Tables and ratios of tooth dimensions in fossil and recent hominids.

Couvering, J. A. van and J. A. Miller

1969 Miocene stratigraphy and age determinations, Rusinga Island, Kenya. Nature 221: 628-632.

> Potassium/argon dating of the lavas of Rusinga Island indicate that most of the vertebrate fossils including *Kenyapithecus africanus* Leakey come from strata of the early Miocene of approximately 18 million years ago. Discusses the geological successions of the Rusinga Island deposits.

Frayer, D. W.

1973 *Gigantopithecus* and its relationship to *Australopithecus*. American Journal of Physical Anthropology 39: 413-426.

ohological pattern of Gigantopithecus mandibles is more similar to Australopithecus than to P. gorilla. Two major points are raised. (1) G. blacki might be considered an aberrant hominid rather than an aberrant pongid. (2) G. bilaspurensis can be considered an equally likely candidate, along with Ramapithecus, for possible hominid ancestry. Comparision of teeth: Gigantopithecus, Australopithecus, and Pan gorilla (Table 1). Tooth measurements and indices for two East African australopithecines and G. bilaspurensis (Table 2). Length/breadth indices for lower molar of G. blacki and G. bilaspurensis and Australopithecus.

Frisch, J. E.
1967 Remarks on the phyletic position of Kenyapithecus. Primates 8: 121-126.

The argument is proposed that Kenyapithecus is best interpreted as a representative of the rich variety of forms characteristic of the hominid adaptive radiation in Miocene times. The specimen does not have to be interpreted necessarily as a remote ancestor of man since many of the features shared with Homo may be parallelisms. Sees the loss of the cingulum in Kenyapithecus as precluding the ancestry of Australopithecus.

Greenfield, L.
1974 Taxonomic reassessment of two Ramapithecus specimens. Folia Primatologia 22: 97-115.

The author argues that two mandibles recently assigned to the genus Ramapithecus should be transferred back to the Dryopithecinae (GSID 199, BM(NH) 15423). He claims that institial wear is a feature controlled by dental age and can be seen in hominids and fossil and recent pongids. It therefore has no taxonomic relevance. The molar wear gradient steepness, mandibular corpus thickness, relative molar breadth, enamel thickening and third molar morphology are also all poor taxonomic markers and show that Ramapithecus does not differ significantly from Dryopithecine specimens.

Jolly, C. J.
1970 The seed-eaters: a new model of hominid differentiation based on a baboon analogy. Man 5: 5-26.

Provides a new model for understanding hominid divergence based initially on a seed-eating econiche. Parallels may be seen in the Gelada baboon whose diet consists essentially of tough small objects. Views the robust australopithecines as representatives of Phase I adaptation, specialization related to the seed-eating complex. The gracile australopithecines, however, should be viewed as early Phase II representatives whose adaptations include recognizable culture, improved bipedalism and some cerebral expansion beyond that seen in the robust group. Favors sinking Australopithecus in Homo as suggested by Robinson (1965).

Kinzey, W. G.
1970 Basic rectangle of the mandible. Nature 228: 289-290.

1973 Ceboid models for the evolution of Hominoid dentition. Journal of Human Evolution 3: 193-203.

The presence of specializations for tough-object feeding in the arboreal cebids such as Cebus apella and Callicebus indicates that hominids may have acquired such specializations in an arboreal habitat before becoming terrestrial. Cites evidence of parallelisms in jaw shape, loss of cingulum, and diet among some of the New World monkeys. Predicts that when postcrania of *Ramapithecus* are discovered that they will not show evidence of bipedal adaptations to a terrestrial environment.

Koenigswald, G. H. R. von

1952 *Gigantopithecus blacki* v. Koenigswald, a giant fossil hominoid from the Pleistocene of Southern China. Anthropological Papers of the American Museum of Natural History 43: 291-326.

Describes the history of the *Gigantopithecus* discoveries, lists of associated fauna, and the geology of various cave sites in Southern China yielding fossils of Pleistocene age. Describes the fossil material consisting of lower 3rd molars, 2nd premolars, upper 2nd molars, a central incisor and canines. Believes that *Gigantopithecus*, as well as *Australopithecus*, were overspecialized side branches of the human line.

1957 Remarks on *Gigantopithecus* and other hominoid remains from Southern China. Proceedings Kon. Akad. Wet. 60: 153-159.

Kurten, B.

1972 Not from the apes. New York: Pantheon Books, 183 pp.

Discusses the possibilities that man on the one hand and monkeys and apes on the other hand have been separate lineages for more than 35 million years, that monkeys and apes descended from the early ancestors of man and may be considered specialized forms, that most of man's history was spent in an arboreal habitat until some 5-10 million years ago, that man has repeatedly speciated all of which except one have become extinct through competition or direct conflict with one another, and that differences in sexual behavior have been overstressed. There may have been little absolute division of labor amongst the sexes.

Leakey, L. S. B.

1967 An early Miocene member of Hominidae. Nature 213: 155-163.

Describes the history of discovereis and controversies over the status of *Kenyapithecus wickeri* and new fossil species from Songhor and Rusinga Island of early Miocene age, named *Kenyapithecus africanus*, type specimen, a maxilla, described in 1951 by LeGros Clark and Leakey as *Sivapithecus africanus*. Includes seven new specimens referred to as the new *Kenyapithecus africanus* species consisting of mandibles and maxillary fragments, isolated teeth and part of a clavicle. Revises the earlier diagnosis for the genus *Kenyapithecus* Leakey 1961.

1968a Lower dentition of *Kenyapithecus africanus*. Nature 217: 827-830.

Describes a mandible with symphyseal region and teeth preserved from early Miocene deposits at Kathwanga, Rusinga Island, Kenya. Specimens Rusinga 1967: 394 supposedly compares closely with other fossils previously described. Describes the morphology of the jaw and teeth between apes and man by the "basic rectangle of the mandible" and offers this as partial proof of the hominid status of K. africanus. Claims ancestry of the Kenyapithecus group in a pre-Miocene form of Proconsul.

1968b Bone smashing by late Miocene Hominidae. Nature 218: 528-530.

Describes fragmented bone assemblages from the Fort Ternan site, examples, the author claims, of depressed fractures "usually associated with 'a blunt instrument'". Describes the recovery of a lava chunk exhibiting several battered edges, and with the appearance of having been used to smash bone. Suspects that Kenyapithecus was, by upper Miocene times, a tool user.

1969a Fort Ternan hominid. Nature 222: 1202.

Argues that Simons' contention of the Fort Ternan fauna as an incursive froup from Eurasia is incorrect. Questions the contemporaneity of the Chinji fauna of the Siwaliks, India, with that of Fort Ternan, Kenya.

1969b Ecology of North Indian Ramapithecus. Nature 223: 1075-1076.

Disagrees with Tattersall's paleoecological reconstruction of the Nagri Mio-Pliocene environment. Argues that most of the fossil faunal evidence can be argued favoring a more open country setting rather than tropical forest.

1970a The relationship of African apes, man, and Old World monkeys. Proceedings of the National Academy of Science 67: 746-748.

Disagrees with Wilson and Sarich (1969) on paleontological grounds that the superfamilies of monkeys and apes separated as late as 30 million years ago. Given if Kenyapithecus wickeri is a hominid then if the biochemical difference between monkey and man are as much as 6x, then the point of divergence between the two forms would be closer to 72 million years.

1970b "Newly" recognized mandible of Ramapithecus. Nature 225: 199-200.

Discusses the history behind the mandible recognized by Pilbeam (1969) as belonging to the genus Ramapithecus. The author claims that Pilbeam originally identified it as Dryopithecus laietanus, claims the specimen is too worn and weathered to make any generic or specific diagnoses and criticizes Pilbeam's criteria for placing it within the Ramapithecus group.

1971 Basic rectangle of the mandible in the Hominoidea. Nature 231: 60.

Argues for the acceptance of Kenyapithecus africanus into the family Hominidae based not only on the shape of the mandible but for "a large number of different characteristics to be seen in the specimens, every one of which is pointed in the same definitie direction". Claims that resemblances between the pongid Proconsul africanus and the hominid Kenyapithecus africanus are to be expected considering both are close to the original common stock of both apes and man.

Pei, W. C.

1957 Discovery of Gigantopithecus mandibles and other material in Liu-Cheng district of central Kwangsi in South China. Vert. Palasiatica (Peking) 2: 65-72.

1962 Quaternary mammals from the Liu-Cheng Gigantopithecus cave and other caves of Kwangsi. Vert. Palasiatica 3: 211-218.

Pilbeam, D.

1966 Notes on Ramapithecus, the earliest known hominid, and Dryopithecus. American Journal of Physical Anthropology 25: 1-5.

Describes the Ramapithecus specimens from India and East Africa and compares their morphology with the contemporary Dryopithecines. The remains of Ramapithecus resemble the equivalent parts of the later Hominidae and contrast with those of the Pongidae. Ramapithecus is the earliest known hominid, some 6 times older than the oldest Pleistocene forms. Dryopithecus is a pongid with three subgenera (Dryopithecus, Proconsul (Africa), and Sivapithecus (India)). Proconsul may be ancestral to the chimpanzee and the gorilla while Sivapithecus is ancestral to the orangutan.

1968 The earliest hominids. Nature 219: 1335-1338.

Discusses the main criteria for placing specimens within the family Hominidae, habitual bipedalism and presence of human dentition, and concludes that Ramapithecus was an early hominid even if evidence is produced which showed that it was not yet a habitual biped. Considers the position of a "Sivapithecus africanus" described by Leakey as an early Miocene hominid and concludes that it is much closer to Dryopithecus species than to Ramapithecus, and thus a pongid. States further that the Miocene fossil record indicates that hominids were recognizably distinct from pongids 14 million years ago.

1969 A newly recognized mandible of Ramapithecus. Nature 222: 1093-1094.

Announces the discovery of an additional mandible located in the fossil primate collections in the British Museum (Natural History) in London. Mandible BM(NH)M 15423 was originally recovered from the deposits of Nagri (upper Miocene) at Domeli in the Salt Range. The mandible consisting of a left piece and most of the horizontal ramus is broken at the symphysis. The canine tooth is reduced and the posterior tooth row is crowded. The fore-shortened and deepened face and jaws suggests that Ramapithecus was capable of powerful chewing.

1970 Gigantopithecus and the origin of Hominidae. Nature 225: 516-519.

Describes the early history of Gigantopithecus discoveries and discusses the taxonomic arguments for and against including the species as a member of the family Hominidae. Discusses the new species of *Gigantopithecus* from India from middle Pliocene deposits and proposes a tentative phylogenetic sequence from *Dryopithecus indicus* (Late Miocene) to *D. giganteus* to *G. bilaspurensis* to *G. blacki*. Reviews the morphological trends within this lineage and compares the dental morphology to that of small-object feeders such as *Theropithecus*.

Prasad, K. N.

1971 Ecology of the fossil Hominoidea from the Siwaliks of India. Nature 232: 413-414.

Gives floral lists for fossils of the Nagri recovered from Haritalyangar and agrees broadly with Tattersall (1969) that the Nagri ecology was one of mixed forest interspersed with streams. Disagrees with Tattersall that the Nagri hominoids were not subjected to heavy predation by social carnivores.

Simons, E. L.

1961 The phyletic position of *Ramapithecus*. Postilla. Yale Peabody Museum No. 57: 1-9.

Discusses the significance of the type specimen of *Ramapithecus*, Y.P.M. 13799, consisting of the right maxilla including the alveoli of the upper incisors and canines, lacking only the upper 3rd molar. According to Simons, Lewis' (1934) conclusions of the hominid resemblances to *Ramapithecus* were correct and Hrdlicka's (1935) rebuttal of the non-hominid characteristics was in error.

1964 On the mandible of *Ramapithecus*. Proceedings of the National Academy of Science 51: 528-535.

Describes newly assigned material to *Ramapithecus* consisting of second right maxilla from Haritalyangar (GSID 185), isolated upper incisor, and right and left horizontal rami of the same mandible (GSID 118, 119) described by Pilgrim as *Dryopithecus punjabicus* 1915, and as *Bramapithecus* by Lewis 1937. Claims the prior binomial for these forms must therefore be *Ramapithecus punjabicus*. Additional three specimens in the Yale Collections (13806, 13813, 13833). Molar teeth tend to be quadrate and crowded rather than anteroposteriorly elongate and spaced out as in *Dryopithecus*. Provides generic diagnosis for the genus *Ramapithecus*.

1969 Late Miocene hominid from Fort Ternan, Kenya. Nature 221: 448-451.

Arguments are presented to substantiate the suthor's claim that *Kenyapithecus wickeri* from East Africa should be placed as a junior synonym of *Ramapithecus*. Compares the fauna between Fort Ternan and the Chinji/Kamlial of India and claims that they are probably contemporary. Discusses morphological similarities between the two forms in the size of the upper central incisor teeth.

Simons, E. L. and D. Pilbeam
1965 Preliminary revision of the Dryopithecinae (Pongidae, Anthropoidea). Folia Primatologia 3: 81-152.

Revises the taxonomic relationships between the members of the family Pongidae and Hominidae (?). Concludes that the Miocene pongids can be considered as a single genus with three geographically divided subgenera: *Dryopithecus* (Europe), *Proconsul* (Africa), and *Sivapithecus* (India).

Tattersall, I.
1969a Ecology of North Indian *Ramapithecus*. Nature 221: 451-452.

Describes the environment in which *Ramapithecus* lived by comparing associated remains of the Nagri Fauna with modern tropical forms. Claims that despite a lack of abundant data the Nagri environment was one of broad rivers, bordered by tropical forests broken by the tree savannahs. Describes the ecological parallels with East Africa *Oreopithecus*.

1969b More on the ecology of North Indian *Ramapithecus*. Nature 224: 821-822.

Reiterates his previous arguments (contra Leakey 1969) for a forest-like environment for *Ramapithecus*. Claims that out of the many thousands of fossils which have come from numerous sites and at many levels within the Nagri Zone, very few are related to savannah-adapted forms. Compares the ecology of the Nagri with the earlier Chinji and later more arid Dhoh Pathan.

Walker, A. and P. Andrews
1973 Reconstruction of the dental arcades of *Ramapithecus wickeri*. Nature 244: 313-314.

The author disputes the rounded dental arcade postulated from other reconstructions of *Ramapithecus* and argues its distinctness from the Dryopithecines. Reconstructs the shape of the mandible of *R. wickeri* (KNM FT 45) by mirror image replica technique and determines that the specimen had very small anterior teeth, as well as posteriorly diverging and nearly straight cheek tooth rows rather than widely separated and cruved tooth rows of modern man. The palate is narrow, the premaxillary region abbreviated and the face broad and flat.

Woo, J. K.
1962 The mandibles and dentition of *Gigantopithecus*. Palaeontologia Sinica 11: 1-94.

Yulish, S. M.
1970 Anterior tooth reductions in *Ramapithecus*. Priamtes 11: 255-263.

Contends that the criteria of anterior tooth height reduction for *Ramapithecus* is not well founded and not significantly

different from modern pongids, and therefore the classification of FT 1271 as a hominid is unjustified on this criteria alona. Provides metrical data on maxillary dentition in *Pan*, *Gorilla* and *Homo sapiens*.

Zwell, M.
1972 On the supposed "Kenyapithecus africanus" mandible. Nature 240: 236-238.

Analysis of KNM RU 2087, described by its author L.S.B. Leakey in 1968 as *Kenyapithecus africanus*. This author explains why he feels this specimen is a Dropithecine. Includes bivariate plots of the lower teeth and a comparison of hominid and pongid characters.